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Activity patterns and foraging behavior of American pikas (*Ochotona princeps*) differ between Craters of the Moon and alpine talus in Idaho

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Abstract.—Range contractions in the Great Basin over the last century suggest that American pikas (*Ochotona princeps*) might be highly sensitive to climate change. However, documentation of pikas residing at relatively warm, low-elevation sites has recently shed new light on the possible resilience of pika populations to warmer ambient conditions when they have access to cooler microhabitats for thermoregulation. To provide insight into the possible behavioral mechanisms of adaptation to warmer habitats, we investigated activity patterns, foraging behavior, and space use of a population of pikas living in an atypical, warmer habitat at Craters of the Moon National Monument and Preserve, an extensive lava flow surrounded by high desert grassland and sagebrush communities in southern Idaho. We compared pika behavior at this site to that of a population in a more typical alpine habitat at Grays Peak in the nearby Pioneer Mountains in Idaho. Specifically, we evaluated and compared activity patterns and foraging behavior of pikas in relation to temperature, time of day, and month. Pikas at Craters of the Moon were less active aboveground during all times of the day from late May until mid-August, compared to those at Grays Peak. Surface temperatures were warmer across the entire season at Craters of the Moon than at Grays Peak, and pikas exhibited a crepuscular activity pattern that coincided with variations in surface temperature at Craters of the Moon. Pikas were the least active during the midday, when the surface temperatures were highest and the insulating effect of the lava tubes (i.e., the difference between surface and crevice temperatures) was most pronounced. Pikas at Craters of the Moon spent less time haying and displayed fewer territorial behaviors than pikas at Grays Peak, but both groups filled a similar number of hay piles. The vegetation community was less diverse and sparser at Craters of the Moon than at Grays Peak, and consequently, the vegetation that was consumed and cached reflected these differences. Our results expand the body of literature about American pikas at their environmental limits, and this study is the first step in identifying the unique suite of behaviors that pikas use to persist in a seemingly inhospitable environment at Craters of the Moon.

Resumen.—La reducción del rango de distribución de la pika americana (*Ochotona princeps*) en el Great Basin durante el último siglo, sugiere que ésta podría ser muy sensible al cambio climático. Sin embargo, el registro de pikas que habitan en sitios relativamente más cálidos y de baja elevación arrojó nueva luz sobre su posible adaptación a condiciones ambientales más cálidas cuando pueden acceder a microhábitats más fríos para su termorregulación. Para conocer sus posibles mecanismos de adaptación a hábitats más cálidos, analizamos los patrones de actividad, de comportamiento de forrajeo y del uso del espacio de una población de pikas en un hábitat atípico y más cálido en el Craters of the Moon National Monument and Preserve ("Monumento y Reserva Nacional Cráteres de la Luna"), un extenso flujo de lava rodeado de pastizales desérticos y comunidades de artemisas al sur de Idaho. Comparamos el comportamiento de la pika, en este sitio con el de una población en un hábitat alpino típico en Grays Peak, en las cercanías de las montañas Pioneer en Idaho. Específicamente, evaluamos y comparamos los patrones de actividad y de comportamiento de forrajeo de las pikas en relación con la temperatura, la hora del día y el mes. Las pikas en Craters of the Moon fueron menos activas en la superficie, durante el día, desde finales de mayo y hasta mediados de agosto, en comparación con las de Grays Peak. Debido a que, la temperatura de la superficie fue más cálidas durante toda la temporada, y a que las pikas exhibieron un patrón de actividad crepuscular coincidente con la variación de la temperatura de la superficie en Craters of the Moon. Las Pikas mostraron menor actividad al mediodía cuando la temperatura de la superficie fue más elevada y el efecto aislante de los tubos de lava (es decir, la diferencia entre la temperatura de la superficie y la grieta) fue más pronunciado. Además, las picas en "Craters of the Moon", destinaron menos tiempo a las actividades de forrajeo y mostraron menos comportamientos territoriales que las pikas de Grays. Sin embargo, ambas poblaciones recolectaron una cantidad similar de pilas de heno. La vegetación fue menos diversa y más dispersa en Craters, comparada con Grays Peak, y en consecuencia, la vegetación que se consumió y almacenó reflejó estas diferencias. Nuestros resultados amplían el cuerpo de evidencia acerca de las pikas americanas dentro de sus límites ambientales, siendo este estudio el primer paso para identificar las conductas de supervivencia de las pikas en un entorno aparentemente inhóspito como lo es Craters of the Moon.

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The American pika (*Ochotona princeps*) is a small mammal that is typically restricted to montane environments on high-elevation talus slopes in the western United States. As a result of their adaptation to these environments, American pikas (hereafter, "pikas") possess several characteristics that could be detrimental to their populations in the face of rising global temperatures (Smith et al. 2004, Beever and Wilkening 2011, Ray et al. 2012). They have a high resting body temperature (40.6 °C) and a low annual reproductive capacity (MacArthur and Wang 1973, Millar 1973, 1974, Smith 1974, Smith 1978). They are also poor dispersers (Smith and Ivins 1983, Smith 1987) and do not hibernate, and so they cache food in hay piles that they amass during the snow-free period and consume that food over the winter (Conner 1983, Dearing 1997). Pikas are also territorial, and small habitat patches typically contain low pika densities; therefore, such populations are subject to stochastic extinction events (Smith and Gilpin 1997, Smith and Nagy 2015, White and Smith 2018).

Range contractions in the hydrographic Great Basin over the last century suggest that pikas might be highly sensitive to climate change (Beever et al. 2003, 2016, Beever and Wilkening 2011, Wilkening et al. 2011, Ray et al. 2012). However, documentation of pikas residing at relatively warm, low-elevation sites has recently shed new light on the possible resilience of pika populations to warmer ambient conditions when they have access to cooler microhabitats for thermoregulation (Beever 2002, Beever et al. 2008, Simpson 2009, Jeffress et al. 2013, Shinderman 2015, Smith and Nagy 2015, Varner et al. 2016, Ray et al. 2016, Smith et al. 2016). Recent studies on populations that inhabit atypical sites on the environmental periphery of their range have shown that pikas employ a suite of behavioral responses to environmental variability, including changes in activity patterns, foraging strategies, habitat use, and use of microrefuges for thermoregulation (Varner et al. 2016, Smith et al. 2016). Pikas are small, and therefore have access to thermal microhabitats where they can decrease the energetic costs of thermoregulation by using behavioral adaptations (Sears and Angilletta 2015, Varner et al. 2016, Smith et al. 2016). Although many studies of pikas in atypical habitats have sought to understand patterns and predictors of occupancy, the behavioral mechanisms that permit pikas to persist at these sites are poorly understood.

In this study, we evaluated the behavioral ecology of a population of pikas at Craters of the Moon National Monument and Preserve (hereafter, "Craters"), an extensive lava flow surrounded by the high desert grassland and sagebrush communities of southern Idaho. We also compared the behavior of Craters pikas to that of a population in a typical alpine habitat at Grays Peak in the nearby Pioneer Mountains of Idaho (hereafter, "Grays"). Craters occurs on an interior range edge for pikas and provides ostensibly marginal habitat conditions (e.g., hotter, drier, and with less vegetation) relative to our current knowledge of the species' habitat requirements (Hafner 1993, Galbreath et al. 2009, Rodhouse et al. 2010, Jeffress et al. 2013). In fact, pikas at Craters experience some of the hottest summer temperatures of any area known to be occupied by pikas (Jeffress et al. 2013). Although MacArthur and Wang (1973) and Smith (1974) demonstrated experimentally that pikas are vulnerable to long-term exposure to high temperatures when prevented from behaviorally thermoregulating (≥25.5 °C), previous studies suggest that pikas use the microtopography in the lava for both thermal cover and caching their hay piles (Rodhouse et al. 2010).

Because Craters is geographically isolated, the population of pikas there might represent a peripheral population that has behaviorally adapted to a unique geological and thermal environment. Extensive surveys have documented pika occupancy at Craters through indirect sign such as feces or hay piles (Rodhouse et al. 2010), but auditory or visual detection of pikas at Craters is difficult. For example, in a survey of 144 sites at Craters, pikas were only seen or heard on 6 occasions (Rodhouse et al. 2010). This elusiveness presents a problem for the study of pika behavior in this atypical habitat.

Our objective was to document the activity patterns, foraging behavior, and space use of pikas at Craters in relation to temperature, time of day, and month, and to compare those data to patterns in a more typical nearby alpine habitat at Grays. Based on anecdotal observations of pikas at Craters and previous studies

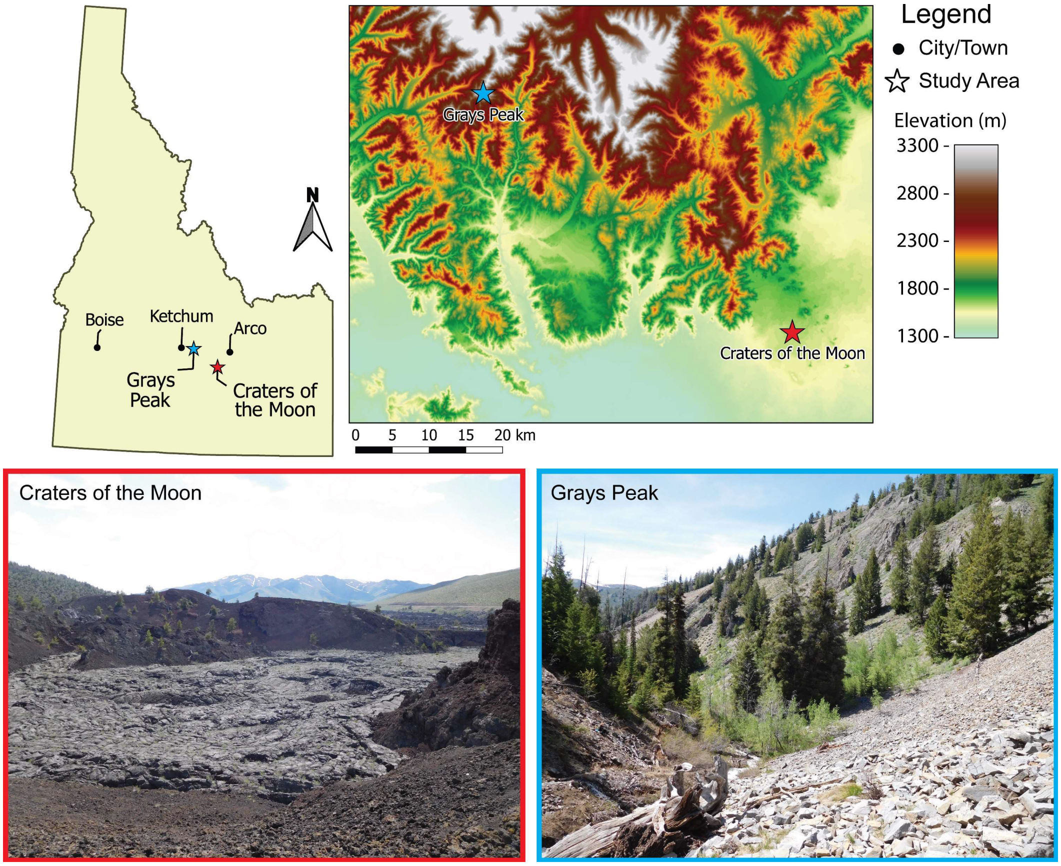

Fig. 1. Location of Craters of the Moon National Monument and Preserve, Idaho, and Grays Peak in the Pioneer Mountains, Idaho (above); photographs of the 2 study sites (below).

on pikas at other atypical sites (Rodhouse et al. 2010, Varner and Dearing 2014a, Varner et al. 2016, Smith et al. 2016), we expected pikas at Craters to be less active aboveground during the day relative to the Grays population, and we expected their activity to be influenced by temperature such that they would be least active during the hottest time of day. At Craters, the vegetation appears sparser, but the growing season longer and the winters milder, than at Grays. Because of these differences, we expected pikas at Craters to use fewer plant species, spend less time haying, and have larger activity centers than those at Grays; we also expected pikas at Craters to make more numerous, modest, and dispersed hay piles than pikas at Grays. This study represents the first step in understanding how pikas at Craters use behavioral modifications to inhabit a highly atypical habitat.

METHODS

Study Area

We conducted this study between May and August 2017 within Craters of the Moon National Monument and Preserve (42.2058° N, 113.5002° W), located in the Snake River Plain of southern Idaho (Fig. 1). Craters contains 1025 km^2 of basalt lava fields consisting of a'a and pahoehoe formations that span an elevational gradient of 1301 m to 1985 m. A'a lava is characterized by rough lava blocks, whereas pahoehoe lava is characterized by a smooth, undulating, or ropy surface. The elevation at our specific study area within Craters was 1800 m. Craters is nearly 330 m below the predicted minimum elevation for pikas at this location, based on previous bioclimatic niche models (Hafner 1993). The lava flows are sparsely vegetated and support shrubs such as fernbush (*Chamaebatiaria millefolium*), Lewis' mock orange (*Philadelphus lewisii*), and antelope bitterbrush (*Purshia tridentata*). They also support forbs, such as scabland penstemon (*Penstemon deustus*) and desert parsley (*Lomatium dissectum*). Perennial grasses at Craters include squirreltail (*Elymus elymoides*) and Idaho fescue (*Festuca idahoensis*). Limber pines (*Pinus flexilis*) are scattered throughout the site as well (Popovich 2006). The area surrounding the lava flows is characterized by high desert grasslands and mountain big sagebrush (*Artemisia tridentata vaseyana*) communities (Popovich 2006). The climate at Craters is semiarid, with most precipitation occurring as snow in the northern region of the park during the winter, and a drought period occurring from June to September. The average 58-year maximum temperature in January was −1.7 °C, and the average minimum was −11.8 °C. The average maximum temperature in July was 29.4 °C, and the average minimum was 7.1 °C. The average annual precipitation was 39 cm, and the average annual snow depth was 15 cm. During our study period, the average high temperature was 32.0 °C, the average low temperature was 6.5 °C, and the total precipitation was 2.1 cm.

For comparison, we also studied pika behavior at Grays Peak (44.8299° N, 115.0062° W), located in the Pioneer Mountain Range within the Sawtooth National Forest, which is north of Craters (Fig. 1). The Grays Peak study area was the nearest documented population of pikas to Craters, approximately 50 km away. The elevation of our study areas at Grays ranged from 2216 m to 2486 m. This habitat is typical of most populations of American pikas, represented by forested areas with patches of talus slopes and lush alpine meadow vegetation (Fig. 1). The area is characterized by spruce-fir, mixed conifer, and quaking aspen (*Populus tremuloides*) ecosystems. At our study site, a creek ran along the base of the talus slope. Common shrubs at the site were common snowberry (*Symphoricarpos albus*), big sagebrush (*Artemisia tridentata*), and American red raspberry (*Rubus idaeus*). Common forbs at the site were stinging nettle (*Urtica dioica*) and western columbine (*Aquilegia formosa*). The average 79-year annual precipitation for Ketchum, Idaho (the nearest weather station to the study site), was 46 cm, and the average 79-year annual snow depth was 20 cm. During our study period, the average high temperature was 23.0 °C, and the average low was 7.2 °C. A total of 5.1 cm of precipitation occurred during our study at Grays.

Temperature

To characterize the thermal environment at each study site, we installed HOBO (Onset Computer Corporation, Bourne, MA) pendant temperature loggers within an active pika area at each site. These data loggers were set to record temperature at 1-h intervals from 27 May 2017 to 31 August 2017. At each location, we placed one temperature logger on a lava (i.e., pahoehoe) or talus surface that was shaded from solar radiation by rocks and a second paired sensor approximately 100 cm below the surface sensor in the natural crevices in which pikas live. At each focal patch, we also measured ambient temperature 2 m above the surface, which was shaded from solar radiation by a radiation shield (Onset Computer Corporation). We used a generalized linear model to evaluate the differences between sites in temperature, time of day, and microhabitat during our observation periods. We included the following factors in the model: site (Craters and Grays), location (either surface or crevice), time of day (morning, midday, and evening), and the 3-way interaction. We followed significant results with pairwise comparisons between locations and sites ($\alpha = 0.05$).

Diurnal and Seasonal Activity

After a period of extensive searching for pikas, we selected 5 focal areas at each study site. The focal areas at Craters were within the North Crater Flow area, and the focal areas at Grays were within a set of talus slopes along the Federal Gulch Trail. After selecting the focal areas, we conducted an initial observation phase. Subsequently, individual observers were positioned so that each person observed the area of approximately one pika home range. We observed 3–5 unmarked focal animals at each study site for a 16-h diurnal period (06:00–22:00), with observations spread over 3–4 d. We attempted to trap and mark pikas at Craters, but despite several hundred trap-hours over 2 summers, we were unsuccessful. To the extent possible, we used ear notches (for 2 animals marked at Grays in 2016) and recognizable physical features (e.g., naturally occurring ear wear) to keep track of individual pikas.

We conducted these surveys for each focal animal once per month in May, June, July, and August 2017, with each observation period at Grays immediately following that at Craters. We also conducted observations from 22:00 to 00:00, but the amount of time we spent observing during this period differed between sites. Although we initially identified 5 focal pikas at each study site, it was difficult to find viewing locations on the lava flow at Craters that allowed us to have a complete view of their home ranges. In addition, focal animals either disappeared or shifted the location of their activity centers between observation periods, which necessitated identifying new focal areas. Therefore, our sample size was variable and small among months. During the first observation period (31 May–06 June), we observed 4 pikas at Craters and 4 at Grays; during the second period (28 June–02 July), we observed 5 pikas at Craters and 3 at Grays; during the third period (17–23 July), we observed 4 pikas at Craters and 4 at Grays; and during the final observation period (09–16 August), we observed 5 pikas at Craters and 4 at Grays.

During the observation periods, we recorded the time of all observed pika activities as defined by Smith and Ivins (1984), which included foraging, haying, surveying, running, grooming, caecatrophy, and territorial and social behaviors such as cheek rubbing (making territorial markings with apocrine glands on the cheeks) and aggression (chasing and fighting). We recorded the number of "feeding events," which we characterized as a feeding bout at a single plant without moving to a different plant; we also recorded the number of "hay trips," which we characterized as gathering a mouthful of vegetation, traveling to a hay pile, and leaving the vegetation within the hay pile. Each plant species that was eaten or hayed during these events was identified and recorded. We recorded the total number of hay piles observed for each focal pika over the entire season as well. We only counted a hay pile if we observed a pika store vegetation in it. Each time a pika was observed at the surface of the lava or talus, we considered the sighting to be an "aboveground visual detection" (see below for quantification in analyses). All short and long calls were tallied during all observation hours, including during nocturnal periods. Short calls are one-note calls. Multiple short calls can occur in the context of predator alarms and duets, a form of antiphonal signing between 2 individuals (Smith and Ivins 1984). Long calls are chattering vocalizations consisting of 30–40 calls, each containing 1–5 song notes, and they are typically given by males only (Smith and Ivins 1984). As in other behavioral studies, pikas quickly habituated to observers (Conner 1983, Smith and Ivins 1984, Smith et al. 2016), and we have no reason to believe that our presence altered their behavior.

For the analyses, we expressed the visual detections of pikas as the number of minutes per hour (0–60) in which the pika was visually detected at least once above the surface of the lava or talus during that minute. The hours were subsequently grouped into 3 time blocks: morning (06:00–10:59), midday (11:00–16:59), and evening (17:00–22:00). To compare activity patterns between Craters and Grays, and to evaluate the influence of surface temperature, month, and time of day on activity patterns, we used generalized mixed effects linear models. We separately evaluated models predicting the minutes of activity per hour, the number of foraging events per hour, and the number of hay trips per hour, and we included the fixed effects of surface temperature during the observation hour, month, time of day, and the 3-way interaction between month, site, and time of day. We also included the focal pika as a random effect. In these models, we used surface temperature and not ambient temperature, because surface temperature is a more biologically relevant driver of microhabitat use for pikas than ambient temperature (Varner and Dearing 2014b). We followed significant results with pairwise comparisons between sites, months, and times of day. We then compared the population-level call rates among sites, months, and times of day using a generalized linear model. We included in that model the effects of site, time of day, and month, the interaction between site and time of day, and the interaction between site and month. We followed significant results with pairwise comparisons ($\alpha = 0.05$).

To augment our observations of pika activity, especially at night, we placed camera traps in pika activity centers or at hay pile sites and positioned them to capture a wide angle of the pika's territory. We placed cameras in 4 pika territories at Craters and 4 at Grays. The cameras recorded pika activity continually from 28 May to 01 October 2017 at Craters and from 07 June to 03 October 2017 at Grays. Each image of a pika was classified by its date and time in order to calculate a detection rate per hour for each individual. We compared the average camera trap detections per hour per individual between sites and time of day by using a generalized linear model. We included in that model the effects of site and time of day, and the interaction between site and time of day. We followed significant results with pairwise comparisons ($\alpha = 0.05$).

Vegetation Sampling and Forage Use

To estimate the species composition of vegetation available to each pika within its territory, we established four 30-m transects originating at right angles from the most active hay pile within each territory. If the location of the hay pile was unknown, a central point of pika activity was used instead. Along each transect, we placed a 1-m^2 microplot on alternating sides every 2 m and visually estimated the percent horizontal cover of each plant species within the plot. Percent cover of each plant species and functional group (i.e., graminoids, forbs, shrubs/deciduous trees, conifers, and mosses) for each territory was averaged among the plots for each month.

We compared the percent of each plant species and plant functional group available within the vegetation transects in each pika's home range to those consumed by each pika while it was foraging and haying during each observation period. We also combined observations of foraging and haying into a single category of plant use to increase our sample size for selection analysis. We then calculated a selection index for each plant functional group from the proportion used by the pikas versus the proportion available on the transects, using Ivlev's electivity index (Jacobs 1974). We classified the functional group as "selected" by pikas if the index was positive and its 95% confidence interval did not overlap zero, "avoided" if the index was negative and the 95% confidence interval did not overlap zero, and "neutral" if the 95% confidence interval overlapped zero.

We compared aspects of both the availability and the use of forage between sites and months. The dependent variables reflecting potential forage resources included the percent of total vegetation cover, the percent of vegetation cover by plant functional group, and the species richness of available plants. The dependent variables describing diet consumed by pikas included the number of foraging and haying events and the plant species richness of diets. Our mixed linear effects models included site, month, and site × month as fixed effects, and individual animal as a random effect. We followed significant results with pairwise comparisons. To compare the foraging and haying for each plant species and functional group, we first averaged the percentages across months and then used a paired *t* test ($\alpha = 0.05$).

Activity Centers

After each observation period, we used a handheld Global Positioning System unit to record the locations where we observed each focal pika during the observation period. Over the 4 observation periods, we obtained locations for 5 pikas at Craters and 4 pikas at Grays. Using ArcGIS (version 10.3; ESRI 2011), we estimated pika activity centers by constructing minimum convex polygons for each activity center. In addition, to characterize the percentage of lava types (a'a or pahoehoe) within each activity center at Craters, we overlaid the activity center polygons on an aerial image of Craters and outlined each lava type within the polygons. Then we calculated the area of a'a within each polygon and the percent of a'a and pahoehoe lava in each home range. We compared the size of the activity centers between sites using a 2-sample *t* test ($\alpha = 0.05$). All statistical analyses were carried out using SAS version 9.3 (SAS Institute Inc. 2011).

RESULTS

Temperature

The average surface and crevice temperatures were warmer during our observation periods at Craters than at Grays ($F_{1,966} = 457.36$, $P < 0.001$). The 3-way interaction among site, location, and time of day was significant ($F_{7,966} = 49.73$, $P < 0.001$). At Craters, the crevice temperature was not significantly cooler than the surface temperature in the morning ($P = 0.09$), but it was significantly cooler in the midday ($P < 0.0001$) and evening periods ($P < 0.0001$; Fig. 2). At Grays, the crevice temperature was cooler than the surface temperature during the morning ($P = 0.0008$), midday ($P < 0.0001$), and evening periods ($P < 0.0001$; Fig. 2).

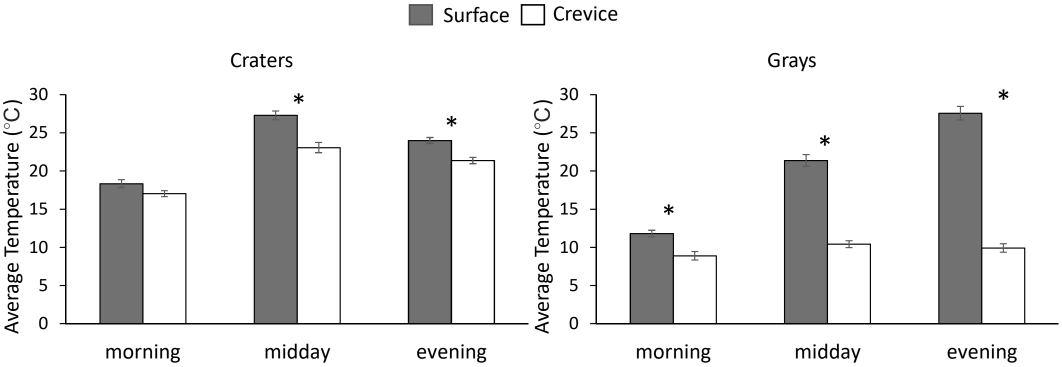

Fig. 2. Average surface and crevice temperatures (±SE) at Craters of the Moon National Monument and Preserve, Idaho, and Grays Peak in the Pioneer Mountains, Idaho, from 27 May 2017 to 31 August 2017. The average surface and crevice temperatures were warmer during our observation periods at Craters compared to Grays ($P < 0.05$). Significant differences ($P < 0.05$) between surface and crevice temperatures within sites are denoted by an asterisk above pairs of bars.

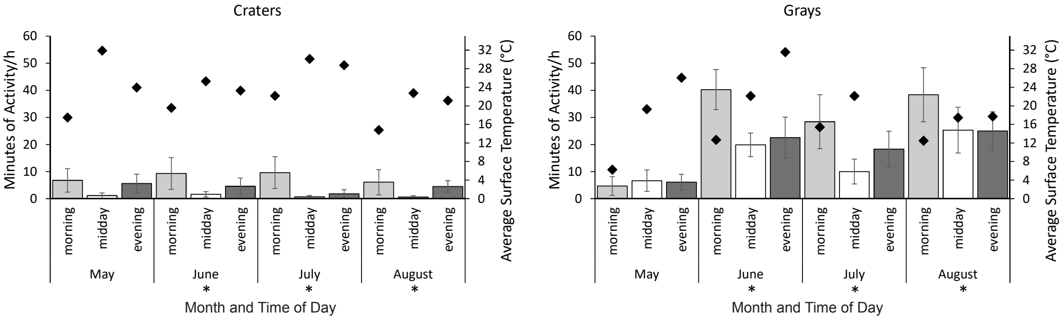

Fig. 3. Average minutes of activity per hour (±SE) of America pikas (*Ochotona princeps*) and average surface temperature (diamonds) by time of day at Craters of the Moon National Monument and Preserve, Idaho, and Grays Peak in the Pioneer Mountains, Idaho, in May (31 May–06 June; Craters: $n = 4$, Grays: $n = 4$), June (28 June–02 July; Craters: $n = 5$, Grays: $n = 3$), July (17–23 July; Craters: $n = 4$, Grays: $n = 4$) and August (09–16 August; Craters: $n = 5$, Grays: $n = 4$) 2017. The minutes of activity per hour of pikas at Craters was significantly influenced by surface temperature, but surface temperature did not significantly influence activity by pikas at Grays. Across the 4 months, there were more detections of pikas during the morning and evening compared to the midday period at Craters ($P < 0.05$ for pairwise comparisons). In June, July, and August, pikas at Grays were more active in the morning ($P < 0.05$ for pairwise comparisons) but equally active during midday and evening. An asterisk below a month indicates that there were significant differences ($P < 0.05$) between the sites in detections per hour for all time periods within that month.

Diurnal and Seasonal Activity

Aboveground activity of pikas was influenced by surface temperature and differed between Craters and Grays. Overall, the minutes of pika activity per hour was significantly influenced by surface temperature ($F_{1,489} = 5.18$, $P = 0.02$), month ($F_{3,489} = 23.59$, $P < 0.0001$), site ($F_{1,489} = 9.93$, $P = 0.002$), and time of day ($F_{2,489} = 9.56$, $P < 0.0001$), and by the 3-way interaction of month, site, and time of day ($F_{17,489} = 8.00$, $P < 0.0001$). Detections per hour of pikas was not significantly different between Craters and Grays during the morning, midday, or evening in May ($P > 0.05$ for all pairs; Fig. 3). However, in June, July, and August, detections per hour during all times of day was significantly lower at Craters than at Grays ($P < 0.05$ for all pairs).

When we examined each site separately, the aboveground activity of pikas at Craters was significantly influenced by surface temperature ($F_{1,270} = 4.36$, $P = 0.04$). As surface temperature increased, the average number of active minutes per hour decreased at Craters ($\beta = -0.14$, SE $= 0.06$; Fig. 3). The number of visual detections of pikas was also influenced by time

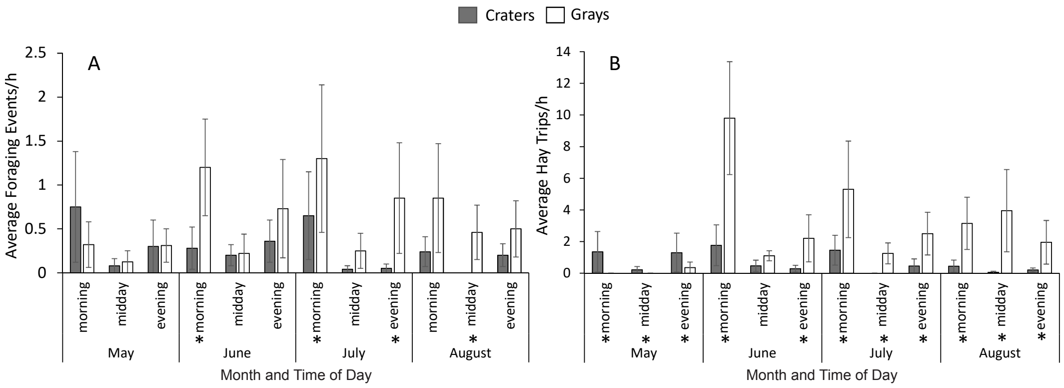

Fig. 4. Average foraging events per hour (±SE; *A*) and average hay trips per hour (±SE; *B*) of American pikas (*Ochotona princeps*) at Craters of the Moon National Monument and Preserve, Idaho, and Grays Peak in the Pioneer Mountains, Idaho, in May (31 May–06 June; Craters: $n = 4$, Grays: $n = 4$), June (28 June–02 July; Craters: $n = 5$, Grays: $n = 3$), July (17–23 July; Craters: $n = 4$, Grays: $n = 4$), and August (09–16 August; Craters: $n = 5$, Grays: $n = 4$) 2017. An asterisk below times of day indicates a significant difference in foraging events or haying trips per hour between sites for that month and time of day ($P < 0.05$).

of day ($F_{3,270} = 1.58$, $P = 0.02$), but not by month ($F_{3,270} = 5.18$, $P = 0.19$). Pikas at Craters displayed a crepuscular activity pattern across the 4 observation periods. There were more detections of pikas during the morning and evening compared to the midday period (morning vs. midday: $t_{270} = -2.81$, $P = 0.005$; morning vs. evening: $t_{270} = -1.65$, $P = 0.10$; Fig. 3).

At Grays, on the other hand, surface temperature had no influence on aboveground activity of pikas during our observation periods ($F_{1,218} = 1.98$, $P = 0.16$), but activity levels varied among months and time of day (interaction effect: $F_{6,218} = 3.06$, $P = 0.007$). Pikas at Grays were significantly less active in the May observation period compared to the other 3 months, and they were equally active during all times of day in May ($P < 0.05$ for all pairwise comparisons; Fig. 3). In contrast, in June, July, and August, pikas at Grays were more active in the morning ($P < 0.05$ for pairwise comparisons) but equally active during midday and evening (Fig. 3).

Overall, foraging activity by pikas did not differ between Craters and Grays ($F_{1,489} = 1.55$, $P = 0.21$) and was not significantly influenced by temperature ($F_{1,489} = 0.51$, $P = 0.48$), but foraging activity differed by the time of day between sites within months (interaction: $F_{17,489} = 1.99$, $P = 0.01$; Fig. 4A). Foraging activity did not differ between the 2 sites during any time of day in May. In June, pikas at Grays fed more frequently in the morning compared to Craters ($t_8 = 3.16$, $P = 0.01$), but they did not differ in their foraging events per hour in the midday and evening. In July, pikas at Grays had more foraging events per hour than pikas at Craters in the morning ($t_8 = 2.47$, $P = 0.04$) and evening ($t_8 = 3.37$, $P = 0.009$), but not in the midday. In August, pikas at Grays had significantly more feeding events at midday compared to Craters ($t_{10} = 2.44$, $P = 0.03$), but feeding events at Grays did not differ from Craters in the morning and evening (Fig. 4B).

Haying activity differed between sites ($F_{1,489} = 9.23$, $P = 0.003$) and was significantly influenced by month ($F_{3,489} = 9.32$, $P < 0.001$), time of day ($F_{2,489} = 4.45$, $P = 0.012$), and the 3-way interaction between site, month, and time of day ($F_{17,489} = 6.14$, $P < 0.0001$) but not by surface temperature ($F_{1,489} = 3.28$, $P = 0.07$). We documented little haying activity by pikas at Grays in May. Hay trips per hour by pikas at Craters was significantly higher during all times of day in May, compared to Grays ($P < 0.05$ for all pairs; Fig. 4). In June, pikas at Grays averaged more hay trips per hour in the morning ($t_8 = 2.57$, $P = 0.03$) and evening ($t_8 = 2.51$, $P = 0.04$) than pikas at Craters, but not during the midday. In July and August, pikas at Grays made more hay trips per hour during all times of the day ($P < 0.05$ for all pairs; Fig. 4).

The average hourly population-level call rate (short and long calls combined) at Craters was

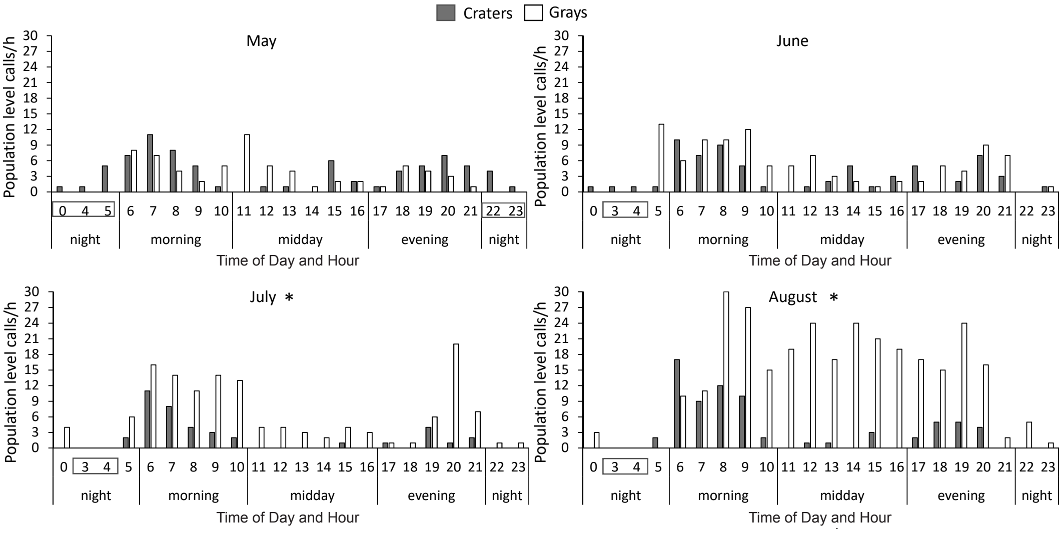

Fig. 5. Total American pika (*Ochotona princeps*) population-level calls per hour (short calls and long calls) at Craters of the Moon National Monument and Preserve, Idaho, and Grays Peak in the Pioneer Mountains, Idaho, in May (31 May–06 June), June (28 June–02 July), July (17–23 July), and August (09–16 August) 2017. The boxes around hours of the day indicate that observations were only conducted at Craters and not Grays. An asterisk next to a month indicates a significant difference ($P < 0.05$) between sites in the population-level call rates during morning, midday, and evening.

2.89 calls/h (SE = 0.65), and the average at Grays was 7.85 calls/h (SE = 0.81). Overall, calls were more frequent at Grays than at Craters ($F_{1,133} = 58.27$, $P < 0.0001$); however, the 3-way interaction effect for site, month, and time of day was significant ($F_{23,131} = 5.51$, $P < 0.0001$). Call patterns followed a crepuscular pattern at both sites in May, June, and July, but pikas called during all hours at Grays in August (Fig. 5). During May and June, there was not a significant difference in the number of call events between sites during the morning, midday, and evening periods ($P > 0.05$ for all pairwise comparisons). During July, there were significantly more calls at Grays than at Craters during the morning ($t_8 = 4.26$, $P = 0.003$), midday ($t_{10} = 8.49$, $P < 0.0001$), and evening periods ($t_9 = 2.24$, $P = 0.05$; Fig. 5). During August, the number of call events did not differ significantly between sites during the morning ($t_8 = 1.78$, $P = 0.11$), but it was higher at Grays during the midday ($t_{10} = 15.65$, $P < 0.0001$) and evening ($t_8 = 3.13$, $P = 0.01$; Fig 5). We had limited data for the night period at Grays, so we could not compare nighttime activity within months, but when we combined all months within sites, there was not a significant difference in the call events per hour between the sites ($t_8 = 1.763$, $P = 0.12$; Fig. 5).

The average detections per hour per individual on our camera traps from late May to mid-October was significantly influenced by the time of day ($F_{3,40} = 6.82$, $P = 0.0008$) and the interaction between site and time of day ($F_{3,40} = 3.16$, $P = 0.03$). The number of detections per hour was not significantly different between sites during the morning ($t_8 = 1.43$, $P = 0.19$), midday ($t_{10} = 1.24$, $P = 0.24$), or evening periods ($t_8 = 0.83$, $P = 0.43$). However, the detections per hour during the night was greater at Craters than at Grays ($t_{14} = 2.44$, $P = 0.03$; Fig 6).

Vegetation Sampling and Forage Use

As expected from habitat conditions, Craters and Grays Peak differed in total plant cover, the percent of plant cover constituting different plant functional groups, the number of plant species, and the specific suite of available plant species. Total plant cover differed between sites ($F_{1,7} = 5.86$, $P = 0.04$) but not between months ($F_{2,11} = 0.06$, $P = 0.94$), nor was there a significant site × month interaction ($F_{2,11} = 0.46$, $P = 0.64$). Across months, Grays had about a threefold higher plant cover ($\bar{x} = 11.39\%$, SE = 2.11%) than did Craters ($\bar{x} = 4.11\%$, SE = 0.63%; Fig. 7). At both sites, shrubs/deciduous trees composed the highest

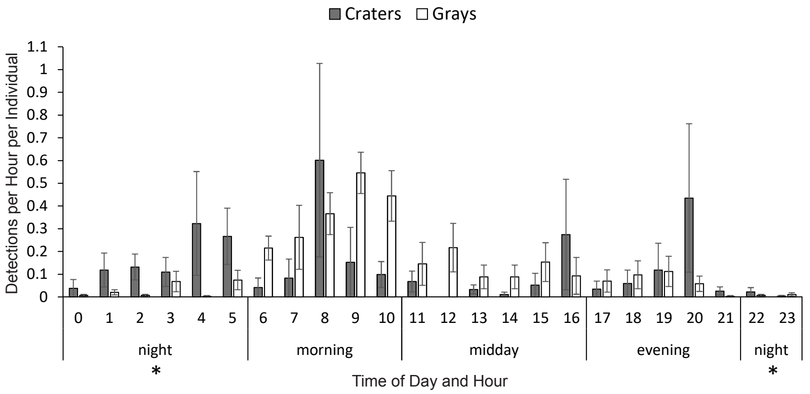

Fig. 6. Average detections per hour per individual (±SE) of American pikas (*Ochotona princeps*) on camera traps placed at Craters of the Moon National Monument and Preserve, Idaho (n = 4), and Grays Peak in the Pioneer Mountains, Idaho (n = 4), from 28 May to 01 October 2017 at Craters and from 07 June to 03 October 2017 at Grays. An asterisk below the time of day indicates a significant difference ($P < 0.05$) in detections per hour per individual between sites within that time of day.

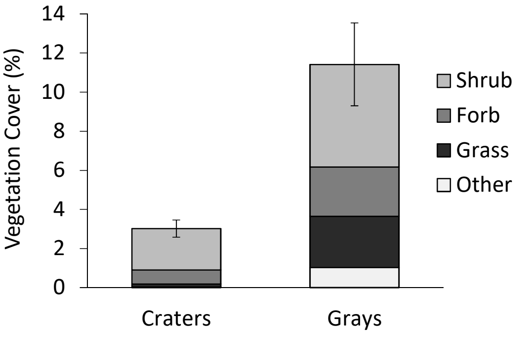

Fig. 7. Total plant cover (±SE) within American pika (*Ochotona princeps*) home ranges at Craters of the Moon National Monument and Preserve, Idaho, and Grays Peak in the Pioneer Mountains, Idaho, in May (31 May–06 June; Craters: n = 4, Grays: n = 4) , June (28 June–02 July; Craters: n = 5, Grays: n = 3), July (17–23 July; Craters: n = 4, Grays: n = 4), and August (09–16 August; Craters: n = 5, Grays: n = 4) 2017. The total percent cover was significantly lower at Craters than at Grays.

percent of plants by functional group (>40%), followed by forbs and grasses (Fig. 7, Table 1); however, a greater percent of available plant cover at Grays consisted of grasses (Grays: $\bar{x}$ = 23%, SE = 3%; Craters: $\bar{x}$ = 4%, SE = 1%; $F_{1,7} = 127.21$, $P < 0.0001$), whereas a greater percent consisted of forbs at Craters (Grays: $\bar{x}$ = 22%, SE = 4%; Craters: $\bar{x}$ = 43%, SE = 4%; $F_{1,8} = 11.33$, $P = 0.01$; Fig. 7). The percent of shrubs/deciduous trees was similar between the sites (Grays: $\bar{x}$ = 46%, SE = 4%; Craters: $\bar{x}$ = 51%, SE = 5%; $F_{1,9} = 0.31$, $P = 0.59$), and the composition of functional groups did not differ with month or site × month (all $P > 0.25$). Conifers and mosses each composed <5% of plant cover at both Craters and Grays.

Craters and Grays differed in the variety of forage available to pikas within their home ranges. Plant species richness varied with site ($F_{1,7} = 6.80$, $P = 0.04$) and site × month ($F_{2,11} = 4.30$, $P = 0.04$), but not by month ($F_{2,11} = 1.28$, $P = 0.32$). Pika home ranges at Grays contained almost twice as many plant species during August ($F_{1,7} = 9.92$, $P = 0.02$) as those at Craters did (Table 1), and the difference in species richness was primarily caused by more shrub/deciduous tree species at Grays in August ($F_{1,7} = 6.92$, $P = 0.03$). Of the 22 plant species (or genera, if species identification was not possible) observed within pika territories at Craters and the 48 species at Grays, only 9% (2 species and 4 genera with unidentified species) were present at both sites (Table 1). Over half of the plant cover in the pika home ranges at Craters consisted of 2 plants: fernbush and sticky cinquefoil (*Potentilla glandulosa*). Four additional shrubs (Lewis' mock orange, *Philadelphus lewisii*; antelope bitterbrush, *Purshia tridentata*; spiny horsebrush, *Tetradymia spinosa*; and oval-leaf buckwheat, *Eriogonum ovalifolium*) and 2 forbs (scabland penstemon, *Penstemon deustus*; desert parsley, *Lomatium dissectum*; Table 1) composed an additional 40% of the plant cover, whereas the other species present were very rare. Unlike Craters, Grays had a more even

TABLE 1. Percent cover of plants, percent of plants used by American pikas (*Ochotona princeps*) in foraging and haying events, and the ranking (1–10 only) of each plant in terms of overall composition at Craters of the Moon National Monument and Preserve, Idaho, and Grays Peak in the Pioneer Mountains, Idaho, in May (31 May–06 June), June (28 June–02 July), July (17–23 July), and August (09–16 August, Craters) 2017. An asterisk (*) denotes a significant difference in the percent foraged and hayed (α = 0.05).

Site	Functional group	Plant species (common name)	Plant species (scientific name)	Vegetation cover		All use events		Foraging events		Haying events	
				% (SE)	Rank	% (SE)	Rank	% (SE)	Rank	% (SE)	Rank
CRATERS	Graminoids	All combined		3.3 (0.8)	—	14.7 (2.1)	—	23.9 (5.4)	—	8.7 (4.2)	—
		Cheatgrass	*Bromus tectorum*	—	—	0.4 (0.4)	—		—	0.5 (0.5)	—
		Squirreltail	*Elymus elymoides*	1.9 (0.8)	10	3.9 (2.1)	6	6.2 (6.2)	5	2.2 (1.6)	8
		Idaho fescue	*Festuca idahoensis*	<0.1	—		—		—	—	—
		Sandberg bluegrass	*Poa secunda*	0.9 (0.5)	—	2.1 (1.3)	9	3.3 (2.4)	8	2.2 (2.2)	7
		Unknown grass		0.4 (0.3)	—	8.3 (2.4)	—	14.5 (4.8)	—	3.8 (2.5)	—
	Forbs	All combined		40.9 (5.3)	—	46.5 (9.7)	—	50.9 (9.8)	—	43.7 (10.5)	—
		Douglas' dustymaiden	*Chaenactis douglasii*	—	—	0.5 (0.5)	—		—	0.8 (0.8)	—
		Rush skeletonweed	*Chondrilla juncea*	<0.1	—		—		—	—	—
		Graygreen thistle	*Cirsium canovirens*	0.3 (0.2)	—	2.8 (2.8)	7		—	4.4 (4.4)	6
		Fleabane	*Erigeron* spp.	1.2 (0.7)	—		—		—	—	—
		Prickly lettuce	*Lactuca serriola*	0.3 (0.3)	—		—		—	—	—
		Desert parsley	*Lomatium dissectum*	6.8 (3.1)	5	6.9 (3.8)	5	8.4 (4.7)	4	7.8 (4.8)	4
		Scabland penstemon	*Penstemon deustus*	7.8 (0.6)	3	12.3 (3.3)	3	9.5 (4.4)	3	16.1 (4.4)	2
		Silverleaf phacelia	*Phacelia hastata*	<0.1	—		—		—	—	—
		Sticky cinquefoil	*Potentilla glandulosa*	24.5 (2.3)	2	22.8 (10.1)	2	*32.0 (10.7)	1	13.7 (5.3)	3
		Unknown forb		—	—	1.3 (0.9)	—	1.1 (1.1)	—	1.0 (1.0)	—
	Shrubs/deciduous trees	All combined		52.2 (5.6)	—	38.3 (8.5)	—	23.7 (5.4)	—	47.6 (13.1)	—
		Saltbush	*Atriplex* spp.	0.5 (0.5)	—		—		—	—	—
		Fernbush	*Chamaebatiaria millefolium*	36.5 (8.7)	1	7.5 (2.8)	4	12.9 (5.6)	2	5.2 (1.9)	5
		Oval leaf buckwheat	*Eriogonum ovalifolium* var. *purpureum*	2.3 (1.1)	8	26.6 (9.7)	1	*4.2 (4.2)	6	39.2 (15.0)	1
		Oceanspray	*Holodiscus* spp.	—	—	0.6 (0.6)	—		—	0.7 (0.7)	—
		Lewis' mock orange	*Philadelphus lewisii*	7.7 (5.9)	4	1.3 (1.3)	10	3.3 (3.3)	7	1.0 (1.0)	10
		Antelope bitterbrush	*Purshia tridentata*	2.8 (1.7)	6	2.3 (1.0)	8	3.2 (2.0)	9	1.5 (0.9)	9
		Spiny horsebrush	*Tetradymia spinosa*	2.4 (1.4)	7		—		—	—	—
		Unknown shrub		1.0 (1.0)	—		—		—	—	—
	Conifers	Limber pine	*Pinus flexilis*	1.5 (1.5)			—		—	—	—
	Mosses	Unknown moss		2.1 (1.4)	9	0.5 (0.5)	—	1.5 (1.5)	—	—	—
GRAYS	Graminoids	All combined		23.6 (0.8)	—	14.5 (2.3)	—	23.1 (8.7)	—	12.1 (1.7)	—
		Brome	*Bromus* spp.	2.3 (1.0)	9	—	—	—	—	—	—
		Sedge	*Carex* spp.	0.5 (0.2)	—	—	—	—	—	—	—
		Fescue	*Festuca* spp.	2.0 (1.9)	—	1.7 (1.5)	8	3.1 (3.1)	6	1.0 (0.8)	—
		Basin wildrye	*Leymus cinereus*	2.0 (0.7)	—	2.7 (1.5)	7	3.6 (3.6)	5	2.9 (1.9)	7
		Reed canarygrass	*Phalaris arundinacea*	2.1 (1.4)	10	1.3 (1.3)	—	—	—	1.4 (1.4)	9
		Bluegrass	*Poa* spp.	0.7 (0.4)	—	0.6 (0.5)	—	0.3 (0.3)	—	0.7 (0.6)	—

TABLE 1. Continued.

Site	Functional group	Plant species (common name)	Plant species (scientific name)	Vegetation cover		All use events		Foraging events		Haying events	
				% (SE)	Rank	% (SE)	Rank	% (SE)	Rank	% (SE)	Rank
GRAYS	Graminoids	Unknown grass		14.1 (1.5)	—	8.1 (1.7)	—	16.2 (5.6)	—	6.0 (2.1)	—
	Forbs	All combined		23.0 (2.8)	—	29.2 (8.7)	—	27.5 (10.8)	—	29.0 (8.4)	—
		Yarrow	*Achillea millefolium*	0.5 (0.5)	—	—	—	—	—	—	—
		Western giant hyssop	*Agastache occidentalis*	—	—	0.3 (0.3)	—	0.7 (0.7)	—	0.5 (0.5)	—
		Umber pussytoes	*Antennaria umbrinella*	0.1 (0.1)	—	—	—	—	—	—	—
		Dogbane	*Apocynum cannabinum*	1.2 (1.2)	—	—	—	—	—	—	—
		Western columbine	*Aquilegia formosa*	4.3 (2.5)	5	14.8 (5.0)	2	14.3 (4.8)	3	14.9 (5.1)	2
		Fireweed	*Chamaenarium angustibolium*	—	—	0.2 (0.2)	—	0.3 (0.3)	—	0.1 (0.1)	—
		Graygreen thistle	*Cirsium canovirens*	0.4 (0.4)	—	—	—	—	—	—	—
		Slim larkspur	*Delphinium depauperatum*	0.6 (0.6)	—	4.2 (2.3)	6	1.9 (1.9)	9	4.7 (2.6)	6
		Aspen fleabane	*Erigeron speciosus*	0.1 (0.1)	—	—	—	—	—	0.1 (0.1)	—
		Arctic alpine forget-me-not	*Eritrichium nanum*	0.7 (0.4)	—	—	—	—	—	—	—
		Bicknell's geranium	*Geranium bicknelli*	0.4 (0.4)	—	0.8 (0.7)	—	0.3 (0.3)	—	0.9 (0.8)	—
		Pacific hulsea	*Hulsea algida*	—	—	0.2 (0.2)	—	—	—	0.2 (0.2)	—
		Ballhead waterleaf	*Hydrophyllum capitatum*	1.2 (0.7)	—	—	—	—	—	—	—
		Cous biscuitroot	*Lomatium cous*	<0.1	—	0.1 (0.1)	—	0.3 (0.3)	—	—	—
		False Solomon's seal	*Maianthemum racemosum*	0.4 (0.4)	—	—	—	—	—	—	—
		Common yellow woodsorrel	*Oxalis stricta*	0.8 (0.8)	—	—	—	—	—	—	—
		Rocky Mountain penstemon	*Penstemon strictus*	1.2 (0.4)	—	1.6 (0.6)	10	1.8 (1.1)	10	1.3 (0.7)	10
		Silverleaf phacelia	*Phacelia hastata*	0.1 (0.1)	—	—	—	—	—	—	—
		Moss phlox	*Phlox subulata*	1.9 (1.1)	—	1.3 (1.3)	—	2.0 (2.0)	7	1.1 (1.1)	—
		Ballhead ragwort	*Senecio sphaerocephalus*	0.2 (0.2)	—	—	—	—	—	—	—
		Western goldenrod	*Solidago lepida*	1.5 (1.5)	—	1.4 (1.3)	—	—	—	1.6 (1.4)	8
		Subalpine spirea	*Spiraea densiflora*	0.8 (0.8)	—	—	—	—	—	—	—
		Dandelion	*Taraxacum officinale*	0.2 (0.1)	—	0.1 (0.1)	—	—	—	0.1 (0.1)	—
		Stinging nettle	*Urtica dioica*	6.6 (5.8)	4	0.4 (0.4)	—	1.1 (1.1)	—	0.1 (0.1)	—
		Unknown forb		—	—	3.5 (2.3)	—	4.8 (2.6)	—	3.1 (2.2)	—
	Shrubs/deciduous trees	All combined		45.9 (6.7)	—	54.8 (10.3)	—	48.5 (18.5)	—	57.3 (8.6)	—
		Rocky Mountain maple	*Acer glabrum*	—	—	0.7 (0.7)	—	—	—	1.0 (1.0)	—
		Saskatoon serviceberry	*Amelanchier alnifolia*	1.0 (1.0)	—	5.3 (5.3)	5	—	—	5.8 (5.8)	5
		Big sagebrush	*Artemisia tridentata*	10.5 (6.3)	2	0.4 (0.4)	—	2.0 (2.0)	8	—	—

TABLE 1. Continued.

Site	Functional group	Plant species (common name)	Plant species (scientific name)	Vegetation cover		All use events		Foraging events		Haying events	
				% (SE)	Rank	% (SE)	Rank	% (SE)	Rank	% (SE)	Rank
GRAYS	Shrubs/deciduous trees	Birch	*Betula* spp.	0.1 (0.1)	—	—	—	—	—	—	—
		Fernbush	*Chamaebatiaria millefolium*	0.1 (0.1)	—	—	—	—	—	—	—
		Parry's rabbitbrush	*Ericameria parryi*	0.4 (0.4)	—	—	—	—	—	—	—
		Common ninebark	*Physocarpus opulifolius*	—	—	0.2 (0.2)	—	—	—	0.4 (0.2)	—
		Quaking aspen	*Populus tremuloides*	1.9 (1.2)	—	7.1 (5.4)	4	15.0 (15.0)	2	6.4 (4.5)	4
		Chokecherry	*Prunus virginiana*	0.9 (0.9)	—	1.1 (1.1)	—	—	—	1.3 (1.3)	—
		Canada gooseberry	*Ribes oxyacanthoides*	2.5 (2.4)	8	0.9 (0.9)	—	0.3 (0.3)	—	1.2 (1.2)	—
		American red raspberry	*Rubus idaeus*	3.8 (1.9)	7	8.4 (6.1)	3	1.7 (1.7)	—	9.0 (6.7)	3
		Shortfruit willow	*Salix brachycarpa*	0.9 (0.9)	—	—	—	—	—	—	—
		Blue elderberry	*Sambucus cerulea*	—	—	0.4 (0.3)	—	0.3 (0.3)	—	0.5 (0.3)	—
		Red elderberry	*Sambucus racemosa*	8.9 (4.5)	3	1.6 (0.7)	9	8.0 (4.9)	4	0.6 (0.4)	—
		Common snowberry	*Symphoricarpos albus*	13.9 (5.0)	1	28.6 (10.4)	1	21.2 (5.8)	1	31.3 (11.5)	1
		Unknown shrub		—	—	—	—	—	—	—	—
	Conifers	All combined		4.2 (3.4)	—	0.7 (0.4)	—	0.7 (0.7)	—	0.7 (0.5)	—
		Ponderosa pine	*Pinus ponderosa*	—	—	0.7 (0.5)	—	—	—	0.7 (0.5)	—
		Douglas-fir	*Pseudotsuga menziesii*	4.2 (3.4)	6	0.1 (0.1)	—	0.7 (0.7)	—	—	—
	Mosses	Unknown moss		3.3 (2.5)	—	0.8 (0.6)	—	0.3 (0.3)	—	0.9 (0.8)	—

vegetation community, with common snowberry (*Symphoricarpos albus*) composing the highest percent of any one species ($\bar{x}$ = 13.9%, SE = 5.0%) by coverage. Half of the plant cover also included 10 additional species, including 4 shrubs (big sagebrush, *Artemisia tridentata*; red elderberry, *Sambucus racemosa*; American red raspberry, *Rubus idaeus*; and northern gooseberry, *Ribes oxyacanthoides*), Douglas-fir (*Pseudotsuga menziesii*), brome (*Bromus* spp.), 2 forbs (western columbine, *Aquilegia formosa*; and stinging nettle, *Urtica dioica*), and moss (Table 1).

Species richness of pika diets reflected the species richness in pika home ranges. The number of plant species used by pikas differed by month ($F_{3,17}$ = 3.51, P = 0.04) and site × month ($F_{3,17}$ = 5.91, P = 0.006), but not by site ($F_{1,7}$ = 3.80, P = 0.09). At Grays, pikas used 4–5 times more species in June, July, and August than in May ($F_{3,10}$ = 4.36, P = 0.03), but species richness in the diet did not vary across months for pikas at Craters ($F_{3,14}$ = 0.15, P = 0.93). In addition, pikas at Grays used more plant species than those at Craters did in August ($F_{1,7}$ = 15.32, P = 0.006), but not in May, June, or July (all $P > 0.08$). Across months, pikas used 15 plant species at Craters, which was 68% of those available (Table 1). Differences in species richness in diets were primarily driven by fewer grass and shrub species consumed at Craters. Ten species were consumed while pikas foraged, 13 were hayed, and 9 were both foraged and hayed. Oval-leaf buckwheat and sticky cinquefoil composed nearly half the plants used by pikas at Craters (Table 1), and 2 grass species (squirreltail, *Elymus elymoides*; Sandberg's bluegrass, *Poa secunda*), 3 forb species (scabland penstemon; desert parsley; graygreen thistle, *Cirsium canovirens*), and 2 shrubs (fernbush and antelope bitterbrush) all composed >2% of the use events (Table 1). All plant functional groups and plant species were used in the same percent for foraging and haying at Craters except sticky cinquefoil, which composed a greater percent of foraging events than haying events (t_4 = 2.80, P = 0.05), and oval-leaf buckwheat, which was used for haying more than for foraging (t_4 = 2.84, P = 0.04).

Across months, pikas used 32 of the 48 plant species available at Grays: 21 were foraged, 28 were hayed, and 17 were both foraged and hayed. Thus, we observed pikas using 65% of the available plant species. Common snowberry, western columbine, and American red raspberry composed the top 50% of the identified used plants, and 1 forb (slim larkspur, *Delphinium depauperatum*) and 2 shrubs/deciduous trees (Saskatoon serviceberry, *Amelanchier alnifolia*; quaking aspen, *Populus tremuloides)* also composed >2% of the use events at Grays (Table 1).

Pikas also used forages differently between Craters and Grays. The number of use events (foraging and haying combined) during a 15-h daylight period differed between sites ($F_{1,6}$ = 6.04, P = 0.04), months ($F_{3,17}$ = 3.57, P = 0.04), and site × month ($F_{3,17}$ = 4.98, P = 0.01). Pikas had 3–8 times more use events at Grays than at Craters in June and August (both P values < 0.004), but both groups had a similar number of events in May and July (both P values > 0.15; Fig. 8). The percent of use events that were haying (rather than foraging) did not differ with site ($F_{1,7}$ = 0.19, P = 0.68), month ($F_{3,19}$ = 2.89, P = 0.06), or site × month ($F_{3,19}$ = 1.99, P = 0.15). Across sites and months, an average of 64% (SE = 6%) of the use events were haying trips. The percent of use of different plant functional groups varied to some degree with site and month (Fig. 8). The percent of use events involving grasses varied with site × month ($F_{3,18}$ = 3.94, P = 0.02), but not with the main effects of site ($F_{1,6}$ = 0.19, P = 0.68) or month ($F_{3,18}$ = 0.41, P = 0.75). Pikas used a greater percent of grasses at Grays than at Craters in July and August, and they used more grasses in May than in June, July, and August at Craters (all P values < 0.05; Fig. 8). The percent of forbs used varied with site ($F_{1,6}$ = 5.97, P = 0.05) and month ($F_{3,17}$ = 5.78, P = 0.007), but not with site × month ($F_{3,17}$ = 0.77, P = 0.53), and the percent of shrubs used varied with site only ($F_{1,6}$ = 6.59, P = 0.05). Pikas at Craters used a greater percent of forbs and a lesser percent of shrubs than those at Grays during May (Fig. 8). Across months and sites, pikas used about 3 times more forbs ($\bar{x}$ = 41%, SE = 5%) and shrubs ($\bar{x}$ = 44%, SE = 6%) as grasses ($\bar{x}$ = 12%, SE = 2%). Conifers and mosses comprised <2% of the pikas' diets.

Electivity indices showed that pikas in both locations used graminoids in greater proportion to their availability (i.e., selected, Craters: $\bar{x}$ = 0.692, 95% CI 0.501 to 0.882; Grays: $\bar{x}$ = 0.252,

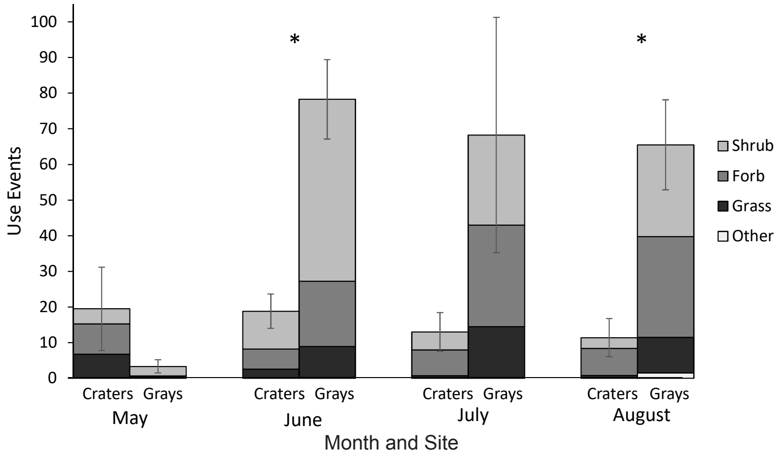

Fig. 8. The number of use events per 15 daylight hours and the percent use of different plant functional groups (shrubs, forbs, grasses, and other) by American pikas (*Ochotona princeps*) at Craters of the Moon National Monument and Preserve, Idaho, and Grays Peak in the Pioneer Mountains, Idaho, in May (31 May–06 June), June (28 June–02 July), July (17–23 July), and August (09–16 August) 2017. Significant differences between sites in the number of use events are denoted by an asterisk above pairs of bars. Pikas used a greater percent of grasses at Grays than at Craters in July and August, and they used more grasses in May than in June, July, or August at Craters (all P values < 0.05). During May, pikas at Craters used a greater percent of forbs and a lesser percent of shrubs than those at Grays did.

95% CI 0.124 to 0.379). Forbs were used in proportion to availability (neutral) at both Craters ($\bar{x} = 0.127$, 95% CI -0.076 to 0.329) and Grays ($\bar{x} = -0.061$, 95% CI -0.501 to 0.379). Shrubs were used in lesser proportion to their availability (i.e., avoided) at Craters ($\bar{x} = -0.389$, 95% CI -0.659 to -0.119) but shrub use was neutral at Grays ($\bar{x} = -0.011$, 95% CI -0.133 to 0.011).

Activity Centers

The average size of activity centers of pikas was nearly 3 times larger at Craters ($\bar{x} = 4015.6$ m^2, SE = 2837.5) than at Grays ($\bar{x} = 1318.1$ m^2, SE = 889.3; $t = -1.61$, $P = 0.07$). Because we did not mark individual pikas, these activity centers possibly belonged to more than one pika. These estimates were also characterized by large standard errors and included an inherent error of ±6 m associated with the handheld GPS units. Pika activity centers at Craters were characterized by mostly pahoehoe ($\bar{x} = 87.17\%$, SE = 11.94%), with a lesser amount of a'a lava ($\bar{x} = 13.71\%$, SE = 11.32%). Four out of 5 pika activity centers at Craters had some a'a lava within their home range. Pikas with a'a in their activity centers were regularly observed to be using this habitat for traveling, surveying, feeding, storing hay, and security or thermal refuge.

We observed no instances of intraspecific aggression and only one instance of cheek rubbing during our observation periods at Craters. In contrast, during the same number of observation hours at Grays, we recorded 36 instances of cheek rubbing, 6 instances of physical aggression (chasing or physically attacking), and 5 instances of kleptoparasitism (stealing hay from another pika's hay pile). On the camera traps at Craters, we also observed a few instances of *Neotoma* stealing hay from pika hay piles.

DISCUSSION

For the first time, we documented differences in behavior between pikas inhabiting a typical, alpine habitat at Grays Peak in the Pioneer Mountains and pikas in a nearby, atypical, low-elevation lava flow at Craters of the Moon National Park and Preserve in Idaho. Pikas at Craters were less active aboveground during all times of the day from late May until mid-August, compared to those at Grays. Furthermore, pikas at Craters spent less time haying and displayed fewer territorial behaviors than pikas at Grays, but both groups filled a similar number of hay piles. However, hay piles at Craters were cryptic from the surface; thus, it was difficult to determine the mass of vegetation in each cache. The vegetation community was less diverse and sparser at Craters than at Grays, and consequently, vegetation that was consumed and cached reflected these differences.

The suppressed midday activity of pikas at Craters suggests that pikas were modifying their behavior to avoid the elevated surface temperatures there. Surface temperatures were warmer across the entire season at Craters compared to Grays, and pikas exhibited a crepuscular activity pattern that coincided with variation in surface temperature at Craters. They were the least active during midday when the surface temperatures were highest and the insulating effect of the lava tubes (i.e., the difference between surface and crevice temperatures) was most pronounced. A previous study at Craters documented that the areas occupied by pikas had more thermally buffering and stable subsurface microrefuges than unoccupied sites did (Rodhouse et al. 2017); other recent studies using temperature sensors within pika habitat have demonstrated that subsurface microrefuge temperatures are cooler than and sometimes decoupled from ambient temperatures (Wilkening et al. 2011, Henry et al. 2012, Millar et al. 2014, Varner and Dearing 2014b, Millar et al. 2016). Our study supports the hypothesis that pikas at Craters remain in subsurface microrefuges in the lava tubes to avoid daytime extreme temperatures and that they use crepuscular activity patterns to avoid midday activity. Our results correspond with a similar study on pikas in another atypical habitat at Mono Craters in California. Like the pikas at Craters of the Moon, pikas at Mono Craters were infrequently active, and activity was concentrated in the early morning and late afternoon when temperatures were cooler than at midday (Smith et al. 2016). Similarly, pikas at warmer, atypical sites tend to be less surface-active overall than those in more typical alpine or montane habitats. For example, pikas at the South Coulee site at Mono Craters were observed during only 10.3% of all observation minutes (Smith et al. 2016), whereas pikas in montane habitats tend to be surface active between 27% and 61% of the time (Conner 1983, Smith and Ivins 1986, Otto et al. 2015, Smith et al. 2016). In our study, pikas at Craters were visually detected during only 7% of the diurnal observation minutes, whereas at Grays they were visually detected during 33% of the observation minutes.

Pikas at Grays were most active in the morning, but their activity patterns were less influenced by surface temperature than the activity patterns of pikas at Craters. In addition, activity varied more across the season at Grays than at Craters. Grays pikas were less active in May compared to later in the season, perhaps because we did not observe any haying behavior in May at Grays. As in our study, the onset of haying occurred earlier in the season at Bodie, a low-elevation arid site in California, relative to a nearby alpine site in the Sierra Nevada (Smith 1974). These patterns likely reflect the delayed phenology at Grays (e.g., snow was still present at the talus toe, and there was little green vegetation near the talus matrix in May). Other studies have documented that pikas are primarily engaged in feeding and reproductive behaviors during that time of year and are not seen haying (e.g., Conner 1983, Smith and Ivins 1984); therefore, it is possible that pikas at Grays were foraging in the snow-free areas above the talus or engaging in reproductive behavior (e.g., maintaining a nursery in the upper reaches of the talus) in areas that were not visible from our position at the toe of the talus. Indeed, pikas in another low-elevation habitat (the Columbia River Gorge) also used forested areas off-talus as a seasonal thermal refuge and as a source of food (Varner et al. 2016, Beever et al. 2017).

The crevice temperatures at Grays were consistently lower and more stable throughout the day compared to the crevice temperatures at Craters. These temperatures could be an artifact of the depth of the sensor placement at Craters (approximately 1 m below the surface), which may not have been deep enough to result in a substantial insulating effect. Our recorded surface and crevice temperatures at Craters were comparable to those at another pika-occupied lava flow, Newberry National Volcanic Monument in Oregon, where the average surface temperature was 37.5 °C and the average crevice temperature was 21.5 °C (Shinderman 2015). In our study at Craters, the average surface temperature was 24.1 °C (range 4.3–41.7) and the average crevice temperature was 19.8 °C (range 5.8–42.4). However, at Newberry and in another study at Craters, temperatures varied substantially across locations (Shinderman 2015, Rodhouse et al. 2017), and we only placed temperature loggers at one hay pile location for each focal animal, so we cannot comment on the temperature variability within territories in our study.

Pikas at both Craters and Grays were active and vocalized at night. We heard calls during most nighttime observation hours at both sites. The average hourly call rate between 22:00 and 05:00 at Craters was 0.89 ± 0.34 calls/h, and the average was 3.71 calls/h at Grays; these rates did not significantly differ between sites. However, there were more detections per hour per pika between 00:00 and 05:00 and between 22:00 and 23:00 on our camera traps at Craters compared to those same times at Grays, suggesting that pikas may have been more active at Craters at night, but not more vocal. Specifically, the cooler temperatures at night at Craters could extend the time available to pikas to engage in activities such as foraging and haying. Similarly, pikas at Mono Craters and at Bodie (both atypical, low-elevation, warmer sites in California) were observed feeding in the middle of the night (Smith 1974, Smith et al. 2016).

To our knowledge, no published research has been specifically dedicated to the study of nocturnal pika behavior. Documenting nocturnal activity of pikas is difficult, even with remote sensing methods like camera traps. Small animals are not uniformly detected by the motion-activated camera traps; detection probability depends heavily on the local arrangement of rocks in the frame. Specifically, it was difficult to capture images of pikas at Craters because the structural complexity of the lava flows limits line-of-sight for both observers and camera traps.

In addition, our location data suggest that pikas at Craters occupy significantly larger activity centers (suggesting larger home ranges) than those at Grays or those mentioned in the published literature; pikas might require more space in this habitat to encompass enough food and suitable microclimate variation for thermoregulation. Pikas at Craters also exhibited less fidelity to a central set of hay piles than pikas at high elevation. Thus, a single camera trap per focal individual may not characterize activity patterns as well as camera traps placed on a hay pile in more typical habitat. Importantly, our data indicate that more research on the nocturnal pika activity at Craters and in other atypical habitats would elucidate the facultative responses of pikas living in warmer environments.

Diurnal foraging and haying activity patterns followed a crepuscular pattern at both study sites, but surprisingly, this pattern was more pronounced at Grays than at Craters in that we observed more feeding and haying activity in the morning and evening at Grays. Although the direct feeding and haying activity that we observed varied greatly among individual pikas within months, pikas at Craters were observed feeding and haying at less than half the rate of those at Grays. At Craters, direct feeding was observed at a rate of 0.27 events/h, and haying was observed at a rate of 0.66 events/h. At Grays, the feeding rate was 0.59 events/h and the haying rate was 2.62 events/h. In a comparable study at Mono Craters, pikas fed at a rate of 0.73 events/h and hayed at a rate of 0.41 events/h (Ray et al. 2016, Smith et al. 2016). Although it is possible that we failed to observe some feeding and haying events at Craters because of line-of-sight limitations, the reduced foraging behaviors (both feeding and haying) at Craters could also be a result of the diurnal thermal environment. Pikas could be shifting their foraging activity to nocturnal periods, as has been observed at Mono Craters and Bodie, California (Smith 1974, Smith et al. 2016). The greatly reduced haying rates at Craters could also be a result of the longer snow-free period at Craters compared to Grays. Craters has a snow-free period 30% longer than and a growing season twice as long as that of Grays; therefore, pikas at Craters might need to rely less on feeding from their hay piles during the winter. Our findings coincide with observations of pikas at Mono Craters; those pikas collected hay at significantly reduced rates compared to pikas in montane regions (Smith et al. 2016). Our pikas also resemble pikas in the Columbia River Gorge in Oregon that hayed significantly less than pikas in typical habitat at the nearby Mount Hood (Varner et al. 2016).

Even though pikas at Craters spent less time haying than pikas at Grays, the average number of discrete hay piles per pika did not significantly differ between the 2 sites. Pikas at Mono Craters and the Columbia River Gorge have been observed scatter-hoarding vegetation rather than having recognizable central-place hay piles (Varner and Dearing 2014a, Smith et al. 2016). Thus, we expected to see similar behavior from the pikas at Craters. On average, we observed pikas at Craters using

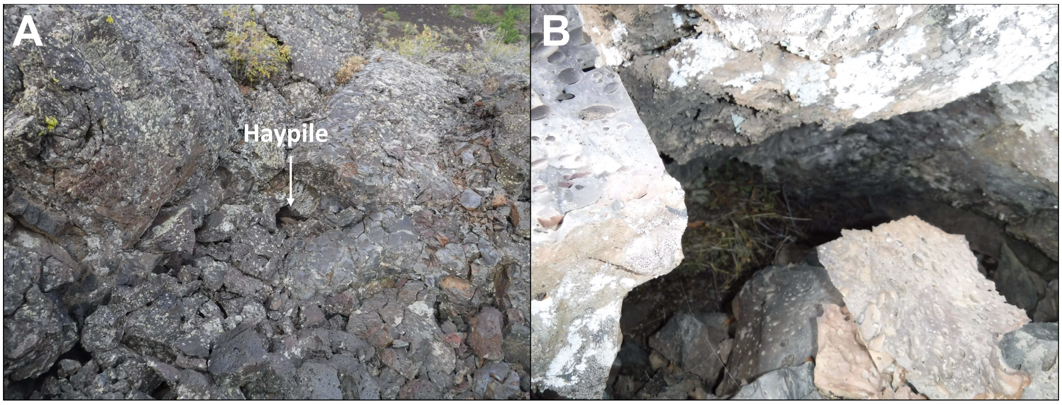

Fig. 9. The entrance to an America pika's (*Ochotona princeps*) hay pile at Craters of the Moon National Monument and Preserve, Idaho (*A*), and a close-up view of the same hay pile (*B*). Hay piles were not immediately identifiable from the surface.

between 1 and 3 main hay piles; however, one pika at Craters was seen scatter-hoarding vegetation in at least 10 locations in addition to using 2 well-formed hay piles. Because of the structural complexity and depth of the lava matrix, we were unable to access or view most of the hay piles at Craters (Fig. 9). In some cases, we were only able to find a hay pile because we saw a pika making frequent hay trips to that location. As a result of these challenges, we were unable to determine whether the total amount of hay stored differed between sites in each season; therefore, we cannot distinguish between the possibilities that Craters pikas cached less vegetation or cached more vegetation at night. These questions are a fruitful area for future research.

Not surprisingly, the availability and diversity of vegetation was lower at Craters, a semiarid lava flow, compared to Grays, a higher-elevation montane site. Grays had about a threefold higher plant cover than Craters did, and it had twice as many plant species as Craters. In both areas, however, pikas used about 60% of available plant species for both feeding and haying, including plant species from all available functional groups. Shrubs and deciduous trees were the most used in both sites, followed by forbs and grasses, and a smaller percent of conifers and mosses. Fernbush covered about 37% of the pika territories at Craters and was the fourth most-used plant. Similarly, fernbush was a positive predictor of pika occupancy at Lava Beds National Monument in California, another atypical mesic site (Ray et al. 2016).

Dietary richness of pikas in both sites reflected the increase in the number of available plant species as the summer progressed. Our sample sizes were too small to detect differences between the summer and winter diets at each site, but no consistent patterns were observed that suggested that pikas preferred to hay plants that were more efficient to transfer (Huntly et al. 1986) or plants that might have enhanced secondary metabolites that would preserve nutritional quality or deter theft of hay piles (Dearing 1996, 1997). However, as in other studies (Dearing 1996, 1997, Varner and Dearing 2014a), the pikas in our study did consume plants known to contain high levels of plant secondary metabolites (e.g., monoterpenes in conifers and sagebrush and phenolics in fernbrush). Pikas also consumed and hayed small amounts of mosses, which are known to be low in digestible energy and high in fiber (Prins 1982, Varner and Dearing 2014a). Our findings are consistent with those from pikas across their range, indicating that pikas are dietary generalists that typically select and consume a wide variety of plants from what is available across space and time (Huntly et al. 1986, Dearing 1996, Smith and Erb 2013).

Our findings suggest that pikas at Craters might use larger areas than pikas in typical alpine habitats. Habitats used by pikas at Craters usually consisted of large expanses of lava flows with extensive crevices that function as cover, and sparse, uniformly distributed vegetation. On the other hand, habitats used by pikas at Grays (and other typical habitats) usually consisted of relatively discrete patches of talus, with forage growing in patches along the edges. Thus, the size of areas used by pikas at Craters might not have been as limited by the size of patches of security and thermal cover as in more typical habitats. Given that home range size often increases as the resource distribution and quality decreases, the activity centers at Craters could reflect the lower abundance and diversity of forage relative to Grays. Over the entire season, Craters had about a threefold lower plant cover within pika home ranges compared to Grays and half as many plant species in July and August. Pikas at Craters might need to use a large area to find enough food, while having access to refuges across the lava for thermal insulation and security cover.

Our results also suggested differences in social behavior that influence territorial defense. During 287 h of observation, acts of aggression by pikas at Craters were never observed, and territorial behavior (i.e., cheek rubbing) was only observed once. Our observations at Craters complement those collected at Mono Craters, where, in 300 h of observation, interspecific aggression was only noted 3 times, and those collected at the Columbia River Gorge, where acts of territoriality or aggression were <1 per 10 h of observation (Smith et al. 2016, Varner et al. 2016). In contrast, in 235 h of observation at Grays, we recorded 36 instances of cheek rubbing, 6 instances of physical aggression (chasing or physically attacking), and 5 instances of kleptoparasitism. Pikas at other typical sites have demonstrated a high degree of territorial behavior (Barash 1973, Svendsen 1979, Smith and Ivins 1984). The large expanse of security and thermal cover at Craters could potentially allow pikas to maintain wider spacing of individual territories, reduce intraspecific encounters, and reduce the need for social interactions, compared to the patchy, discrete talus and meadow habitats available at Grays and other typical environments.

Finally, we found pikas using a variety of lava formations and types within activity centers. Although pahoehoe lava made up the majority of the area in which we observed pikas at Craters (as expected based on occupancy surveys; Rodhouse et al. 2010), we also observed 4 out of 5 pikas actively using a’a lava for traveling, surveying, feeding, storing hay, and refuge (security or thermal). Previous studies at Craters indicated that pika site occupancy was 10 times greater in pahoehoe than in a’a, and that thermal conditions were substantially more stable in pahoehoe relative to a’a (Rodhouse et al. 2010, 2017). Because we did not specifically document frequency of use of the 2 lava types, the value of a’a to pikas at Craters and other volcanic sites requires further study.

Our study documented behavior and habitat conditions of pikas at an atypical lava flow compared to the closest-available typical pika population during the same time period. This paired study design allowed us to standardize conditions for comparing diurnal and seasonal effects on behavior between sites. However, our study was limited by low pika density within our targeted sites and by the fact that we observed unmarked animals over 3- to 4-d periods. Therefore, our study is only the first step in identifying the unique suite of behaviors pikas use to persist in a seemingly inhospitable environment.

Our results expand the growing body of literature on pikas at their environmental limits (e.g., Severaid 1955, Smith 1974, Peacock and Smith 1997, Massing 2012, Smith and Nagy 2015, Varner et al. 2016, Smith et al. 2016, Millar et al. 2018). However, it is important to note that the ability to behaviorally adapt to suboptimal conditions does not preclude the possibility that climate change will have negative effects on pikas. As Beever et al. (2017) noted, behavioral flexibility can offer pathways for species to persist in changing climatic conditions, yet physiological limitations, trade-offs with other fitness-related activities, and the range of environmental conditions over which behavior is flexible might still limit species in future climate change scenarios. At Craters, pikas are largely restricted to structurally complex, sparsely vegetated pahoehoe lava flows in the northern portion of the monument, and climate change could erode the size and connectivity of suitable habitat patches (Rodhouse et al. 2010). The future distribution of pikas, as predicted by species distribution models, varies widely due to local environmental idiosyncrasies and site-specific factors; these factors include habitat connectivity and habitat configuration, which both can be modified by climate change (Jeffress et al. 2013, Schwalm et al. 2016). Our results suggest that at least some populations of pikas can adjust their behaviors to accommodate variation in food resources and macroclimates, yet future research is needed to better understand the extent to which pikas can modify their behavior to accommodate a variety of biogeographic and environmental contexts.

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