BioOne RESEARCH EVOLVED

Patterns of Selective Caching Behavior of a Generalist Herbivore, the American Pika (*Ochotona princeps*)

Author(s): Justine A. Smith and Liesl P. Erb
Source: Arctic, Antarctic, and Alpine Research, 45(3):396-403. 2013.
Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado
DOI: http://dx.doi.org/10.1657/1938-4246-45.3.396
URL: http://www.bioone.org/doi/full/10.1657/1938-4246-45.3.396

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Arctic, Antarctic, and Alpine Research, Vol. 45, No. 3, 2013, pp. 396–403

Patterns of Selective Caching Behavior of a Generalist Herbivore, the American Pika (*Ochotona princeps*)

Justine A. Smith and*
Liesl P. Erb†

*Corresponding author: Department of Environmental Studies, University of California, Santa Cruz, 1156 High Street, Santa Cruz, California 95064, U.S.A.
Jsmith5@ucsc.edu
†Department of Ecology and Evolutionary Biology, University of Colorado, UCB 334/EE Biology, Boulder, Colorado 80309, U.S.A.

Abstract

Caching decisions have been studied for many species, but large-scale variation of selective preferences due to environmental heterogeneity has rarely been examined. We investigated large-scale patterns of selective caching behavior in the American pika (*Ochotona princeps*), a non-hibernating generalist herbivore that caches vegetation in haypiles to serve as winter food. At 13 sites throughout the southern Rocky Mountains, we identified the three most common available and cached plant species and analyzed them for dietary quality. Selectivity at each site was measured as the difference between average quality of the most common cached and available vegetation. Pikas consistently cached materials of higher quality than the most common available vegetation. Selectivity for high nitrogen corresponded to quality of available plants and site summer temperature, whereas selectivity for high water content was negatively correlated with elevation. Our results indicate that pikas cache a variety of plant materials while using different selectivity cues, illustrating the complexity of pika caching behavior across a range of environmental conditions and forage values. Future studies on caching behavior should take into account differential selectivity due to environmental heterogeneity.

DOI: http://dx.doi.org/10.1657/1938-4246-45.3.396

Introduction

Arctic and alpine ecosystems present unique challenges for species due to extreme seasonality and unpredictable resource availability. Species that dwell in these environments are forced to adopt strategies to survive extensive food shortages. Whereas some animals use physiological strategies to cope with periods of low food availability, others must rely on behavioral adaptations (Craig et al., 1979; Katz, 1974). Food caching is one behavioral strategy that has evolved to ensure the availability of food during energetically stressful periods (Smith and Reichman, 1984). When selecting food items for storage, caching species often take into account energy content, nutritional quality, and perishability of vegetation to ensure that the cache will sustain its gatherer through times of need (Gendron and Reichman, 1995; Hadj-Chikh et al., 1996; Lewis, 1982). Despite a rich literature on caching behavior, caching decisions have rarely been tied to environmental heterogeneity across space. Large-scale variation of selective preferences is poorly understood, particularly as it relates to topographical and climatic features. Given that current global environmental changes are predicted to drastically alter plant community composition in alpine systems (Guisan and Theurillat, 2000), this information gap must be closed. This study begins to examine patterns of selective foraging behavior across space in the American pika (*Ochotona princeps*).

The American pika, a lagomorph endemic to western North America, is a generalist herbivore that caches vegetation throughout summer and early autumn in haypiles. These caches are stored in rocky crevices in talus (broken rock) slopes, the pika's preferred habitat. Pikas do not hibernate, so they collect vegetation to serve as a winter food supply when harsh environmental conditions prevent foraging (Conner, 1983). Pikas are an ideal study species for investigating selectivity, as each individual maintains a separate territory and thus has a restricted subset of vegetation available in the form of the plants adjacent to or within the talus forming that territory (Huntly et al., 1986; Roach et al., 2001). We chose this species to explore large-scale patterns of selectivity because pikas exhibit limited dispersal between sites, minimizing lateral behavioral transfer across our study area. In addition, forage quality or quantity has proven important to pika population persistence throughout the American West (Wilkening et al., 2011, Erb, unpublished data).

Pikas vary in the forage species they consume and cache across their range and are considered generalists (Smith and Weston, 1990). However, at particular sites, pikas have been documented to preferentially harvest some plants extensively while ignoring other available plant species (Krear, 1965; Millar and Zwickel, 1972). To date, hypotheses on which vegetative characteristics influence forage selection are diverse and largely site-specific. Decades of research suggest alternative forage preferences based on plant size and morphology (Huntly et al., 1986), spatial distribution of plants (Roach et al., 2001), nutrition (West, 1980), presence of secondary compounds (Dearing, 1996), and novelty (Ivins, 1984). Previous studies are conflicting in the variables found to influence selection and the degree to which they do so. The diversity of selective caching explanations in this species indicates that pika decisions are complex and may vary across space and time.

Incongruity regarding pika forage preferences may reflect variation in climatic and topographic conditions among previous studies, each limited to one or two adjacent sites. Environmental heterogeneity might impact both the degree of selectivity employed by pika populations and the preference for different plant characteristics at each site. Our objective was to provide an evaluation of selective caching behavior by pikas throughout the southern Rocky Mountains and, as such, to explore how site-specific variables may influence caching preferences.

© 2013 Regents of the University of Colorado
1523-0430/6 $7.00

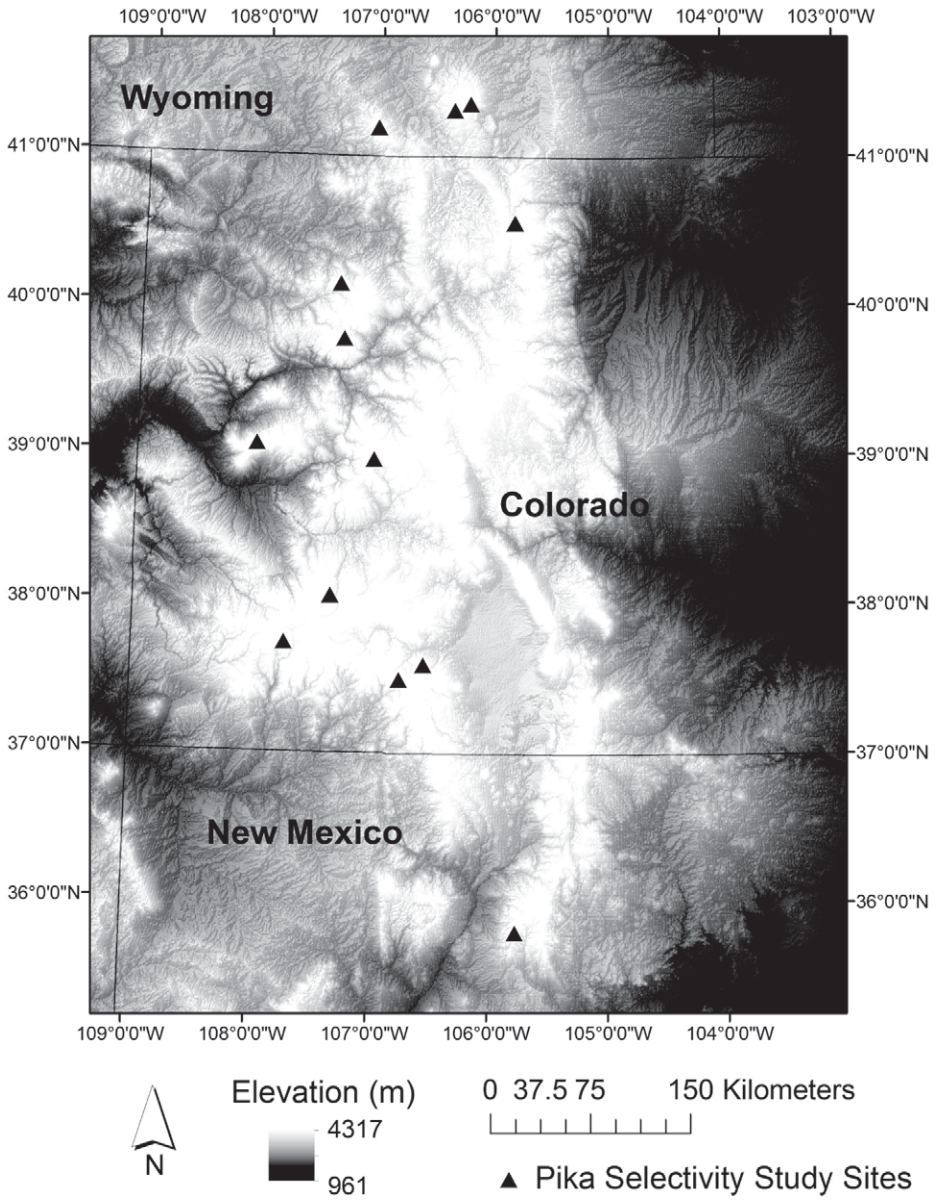

FIGURE 1. Map of sites sampled to determine dietary preferences of *Ochotona princeps*.

Here we perform large-scale analyses of pika caching behavior as it relates to site-specific environmental conditions. Pika populations each experience a different combination of food choices based on environmental controls on plant communities. Complex interactions among climate, topography, soils, and biotic communities in mountainous environments yield heterogeneous landscapes with great variation in vegetation composition (Cairns and Malanson, 1998). Because topographical and climatic features are often related to plant composition and nutrient content (Cairns and Malanson, 1998; Körner, 1998), they may influence the foraging behavior and degree of selectivity exhibited by different pika populations. In addition, climate is likely to alter foraging behavior by restricting access to forage in harsh conditions and shifting the nutritional inputs that are limited in a given population. To test the relationship between caching selectivity and environmental variables, we investigated the following questions:

- Q1: Do pika populations exhibit preferential caching behavior based on dietary elements across a large geographic scale?
- Q2: Does the degree of selectivity depend on the quality of available vegetation at a site?
- Q3: Can the degree and nature of selectivity patterns be explained by broad measures of environmental variation?

Methods

STUDY AREA

Thirteen sites known to be occupied by pikas both currently and historically (pre-1980) were selected via random sample stratified by latitude and elevation from a larger sample of 69 such sites in the southern Rockies. The 13 study sites ranged in latitude from the southernmost tip of the distribution of *O. princeps* at Nambe Lake, New Mexico (35°79′N), to the Snowy Range of the Medicine Bow Mountains, Wyoming (41°35′N; Fig. 1). Elevations ranged from 3036 m at Trap Lake, Colorado, to 3717 m at Nambe Lake, New Mexico. The order of site visits was designed to minimize phenological impacts on plant quality. Visits were timed to allow

for an estimated three-day delay in plant development per 100 m in elevation or one degree latitude (Schwartz and Caprio, 2003; Bowman et al., 1999). Based on these calculations, all sites were visited at approximately the same phenological stage (± 3 days), with southern, lower-elevation sites visited early (in July) and northern, high-elevation sites visited later in the season (August).

DATA COLLECTION

Haypiles were detected by walking transects across the entire talus patch, perpendicular to the dominant aspect of the habitat. The first transect was set 10 m above the lowest elevation of the talus within the site. Additional transects were surveyed upslope at 60 m ground-level intervals as long as talus was present. If any one transect would intersect more than 200 m of contiguous talus, only 200 m of the transect was surveyed. In this case, the full transect consisted of three sub-transects: two sub-transects of 50 m, each extending inward from the edges of the talus patch, plus one sub-transect of 100 m, positioned in the center of the talus patch. This subset was chosen to best represent vegetative characteristics of the site, as most vegetation exists near the talus edge.

Two observers walked along each transect, one looking for haypiles up-slope and one looking down-slope. Detected fresh haypiles were dissected to determine plant composition, and only green vegetation was identified to ensure that the vegetation analyzed had been gathered in the current year. All accessible haypile vegetation was extracted and sorted by species. The three most common plant species present in each haypile were identified, and their relative volumes in the haypile were estimated based on visible biomass. Graminoid species were lumped into a single category (Dearing, 1996), and all other taxa were identified to species using Weber's *Rocky Mountain Flora* (1976). It is standard practice for alpine graminoids to be lumped in haypile analyses because it is assumed that they have similar nutritional content from the perspective of the pika (Dearing, 1996; Gliwicz et al., 2006). All detected fresh haypiles were surveyed, and all vegetation was returned to its original haypile following dissection. We determined the three most commonly cached species at each site by counting occurrences across haypiles.

Vegetation surveys were conducted adjacent to three randomly selected haypiles within each site. Our sampling framework was designed to capture available vegetation most accessible to pikas, which often build haypiles along talus edges. We used the point intercept method (PIM) to estimate individual species proportions of available biomass. Point counts from the PIM are highly correlated to biomass in many ecosystems, including montane meadow plant communities (Bråthen and Hagberg, 2004; Jonasson, 1988). Three 50-m vegetation transects were sampled around each haypile, each running perpendicular to the dominant aspect at the haypile, as in Wilkening et al. (2011): the first transect was centered on the haypile and extended 25 m horizontally to each side, and two parallel transects were positioned 15 m up-slope and 15 m down-slope from the same haypile. A vertical marker was positioned at every meter along each transect, and plant species touching this marker were identified and recorded along all nine 50 m transects sampled within each site. Total counts were made of each taxon's occurrence in the vegetation survey, and the three most abundant available plants were calculated from data averaged across all transects at each site. Plants were identified to species for all taxa but graminoids, which, as in haypile surveys, were treated as a single taxon.

At each site, samples of the three most common plant species in haypiles and the three most common available plant species were collected from growing vegetation. For the remainder of this paper, ''common'' available and cached species will refer to these fresh samples collected representing common available and hayed species. Collection from intact plants was standardized by cutting all specimens at ground level and in full sun to eliminate the influence of dew on initial weights and minimize environmental variation caused by differences in light availability (Bowman et al., 1999). In addition, multiple source plants of each species were selected from the area within 30 m of a pika haypile at each site. Samples from intact plants were collected in paper bags and immediately weighed to the nearest 0.25 g with a 60 g spring scale (PESOLA AG, Rebmattli 19, CH-6340 Baar, Switzerland). Paper bags were weighed prior to the addition of the samples, and this weight was subtracted from the total mass to determine the wet weight of each sample.

VEGETATION ANALYSIS

Of potential plant characteristics that could influence selectivity, we focused on indicators of plant quality, examining nitrogen content (as an approximate measure of protein; AOAC, 1965) and water content. Plant samples were thoroughly air-dried in a mesh bag at the University of Colorado and then dried in an oven for 24 h at 60 °C. Samples were weighed immediately after drying to assess water content. Water content was computed as the total percent weight lost during drying (weight at harvest vs. weight following oven drying). Using liquid nitrogen and a mortar and pestle, 0.5 g of each sample was finely ground. Adding liquid nitrogen does not change the chemical composition of the sample, but facilitates the grinding process (Torregrossa and Dearing, 2009). We packaged 3 to 5 mg of each sample in 5×9 mm tin capsules and run though a Costech ECS 4010 elemental CHNSO analyzer (Costech Analytical Technologies, Valencia, California) to determine percent nitrogen.

STATISTICAL ANALYSIS

As an estimate of the overall contribution of a plant species to the vegetation available at site k, the relative proportion of each focal species was determined by:

$$A_{ik} = n_i/N, \quad (1)$$

where n_i is the number of detections of species i along the vegetation transects and N is the total number of individual plants detected along the transects.

The proportion of species i at each site k relative to all cached material observed in haypiles was characterized by:

$$C_{ik} = \Sigma(h_j p_i)/\Sigma(h_j), \quad (2)$$

where h_j = size of haypile j and p_i = estimated proportion of species i of the three most common plants cached in haypile j. The relative size of each haypile was estimated in units of loose (observed) dry volume, each unit being $10 \times 10 \times 30$ cm (C. Ray, personal communication).

Nitrogen content (Y_k), and water content (Z_k), at site k of available and cached vegetation in the environment ($m = 1$) or in haypiles ($m = 2$) were characterized by the following equations:

$$Y_{km} = \Sigma(N_i)S_m \quad (3)$$

$$Z_{km} = \Sigma[1 - (d_i/w_i)]S_m, \quad (4)$$

where $S_m = [A_{ik}, C_{ik}]$, N = nitrogen (% weight), d = dry weight (in mg), and w = wet weight (in mg).

The selectivity index for each variable at a given site was calculated as:

$$I = (\delta_C/\delta_A) - 1, \quad (5)$$

where $\delta_A = [Y_{k1}, Z_{k1}]$ and $\delta_C = [Y_{k2}, Z_{k2}]$ depending on variable of interest. Therefore, the selectivity index at a site for a given dietary variable is the residual value between the cached to available vegetation quality ratio and 1, the expected ratio given no selectivity. The relative magnitude of the selectivity index changed with each variable, depending on variance within a sample set. A positive selectivity index represents selective caching for higher values of the given nutritional factor than are found in available vegetation. A negative selectivity index represents selective caching for lower values of the given nutritional factor than are found in available vegetation. Zero is the expected value given no selectivity.

Because we did not expect the ratio of cached to available vegetation quality to be distributed normally, all analyses were conducted using the log transformation of the selectivity index:

$$\log(I) = \log(\delta_C) - \log(\delta_A). \quad (6)$$

To address our first question, if pikas exhibit selective caching behavior across sites, we used paired *t*-tests to determine if nutritional composition of common plants found in haypiles was different from common available vegetation. To address our second question, if degree of selectivity depends on vegetation quality, we tested if the slope of the relationship between cached and available vegetation was significantly different from 1 by calculating the slope confidence interval:

$$CI = \beta_1 \pm t_{\alpha/2}SE(\beta_1) \quad (7)$$

where β_1 is the slope of the relationship, $t_{\alpha/2}$ is the t value of the coefficient β_1 at significance level α, and $SE(\beta_1)$ is the standard error of β_1 (Montgomery et al., 2012). We calculated confidence intervals at α values of 0.05 and 0.01 for each vegetative characteristic.

To investigate our third question, if patterns of selectivity are related to environmental factors, we tested if selectivity was related to elevation, mean summer temperature, and total annual precipitation through linear regression. We chose mean summer temperature as the most appropriate measure of temperature because chronic heat stress is thought to limit foraging time in pikas (MacArthur and Wang, 1974). Mean summer temperature was calculated as the mean temperature recorded in the months of June, July, and August by HOBO U-series data loggers (Onset U10-003) placed in pika haypiles. We chose total mean annual precipitation as the best precipitation measure, because winter and spring snow runoff and summer rains all contribute to summer plant growth. Annual precipitation was obtained from PRISM Climate Group (2010). Only univariate models were tested due to sample size constraints.

Results

Of the 13 sites analyzed, 133 haypiles were dissected, and 60 plant samples were collected and analyzed. In no cases were the identities of the top three available and cached taxa identical. Graminoids were among the most common available and cached species at all but one site, comprising the most abundant available vegetation at 92% of sites and the most abundant cached vegetation at 69% of sites. Forb composition was highly heterogeneous across our study area; only 25% of the available forb species recorded were common at multiple sites. The lists of common available and cached species and values of nutritional quality at each site are presented in the Appendix.

PREFERENTIAL CACHING BEHAVIOR AMONG SITES

We found a positive relationship between common available and cached vegetation for nitrogen content ($R^2 = 0.388$, $P = 0.023$; Fig. 2, part a) and water content ($R^2 = 0.757$, $P = 0.0001$; Fig. 2, part b). Cached vegetation at a site was significantly higher in quality than environmental vegetation in terms of nitrogen content ($t = -3.21$, *d.f.* = 12, $P = 0.008$) and water content ($t = -5.20$, *d.f.* = 12, $P = 0.0002$), resulting in positive selectivity indices for each vegetative characteristic at most sites (Table 1).

DEGREE OF SELECTIVITY AND AVAILABLE VEGETATION QUALITY

The slopes of the relationship between quality of cached and available vegetation for nitrogen content ($\beta = 0.521$, $P < 0.05$, 95% CI 0.134 – 0.909) was significantly less than 1, suggesting that selectivity for higher quality plants decreased as the quality of available plants increased. The slope of the relationship between water content in common cached vegetation and available vegetation was not significantly less than 1 ($\beta = 0.877$, $P > 0.05$, 95% CI 0.583 – 1.171), indicating that as water content in available vegetation decreased, pikas did not compensate by significantly increasing selectivity.

PATTERNS OF SELECTIVITY AND ENVIRONMENTAL VARIATION

Average summer temperature had a positive relationship with selectivity for nitrogen content ($R^2 = 0.433$, $P = 0.020$; Fig. 3, part a). The selectivity index for nitrogen content did not show a strong relationship with elevation or precipitation ($P > 0.05$). There was a negative relationship between elevation and the selectivity index for high water content ($R^2 = 0.366$, $P = 0.029$; Fig. 3, part b). We did not find a relationship between percent water content in common available vegetation with elevation ($P > 0.05$); therefore, available water content cannot explain the variability we observed in selectivity along an elevational gradient. The selectivity index for water content did not show a strong relationship with temperature or precipitation ($P > 0.05$).

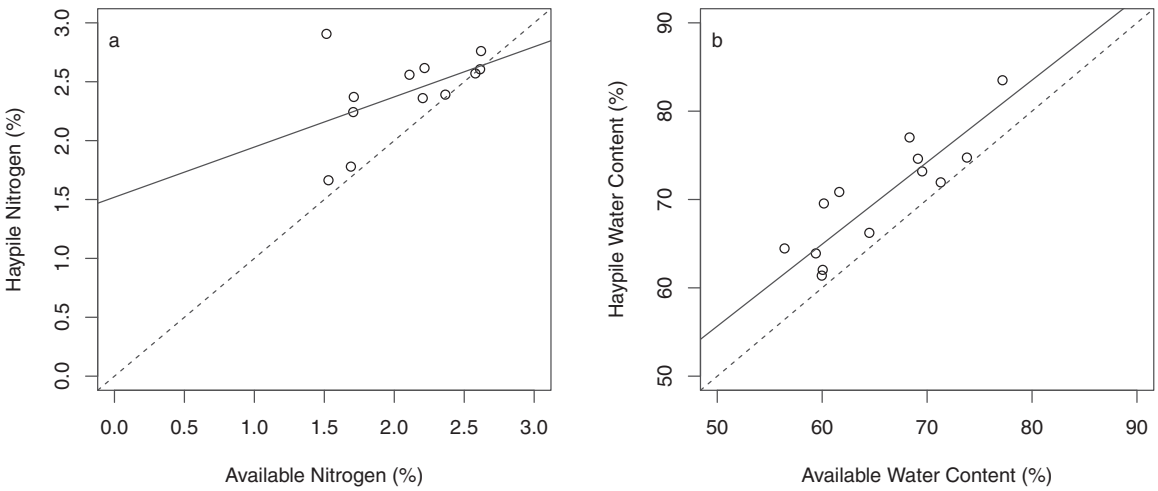

FIGURE 2. Relationship between the quality of the three most common cached plants and the quality of the three most common available plants for: (a) % nitrogen content; and (b) % water content. The solid line is the best-fit linear regression line. The dashed line is the 1-to-1 relationship expected given no selective haying behavior. Each point represents the weighted average plant quality at an individual site.

Discussion

In this study, pikas cached a large variety of plants across a vast elevational and latitudinal range. Graminoids were consistently among the most common available plants and almost always found in haypiles. While it is common practice to group graminoids (Dearing, 1996), we acknowledge that this practice may partially explain the prevalence of graminoids as one of the three most common available and cached plants in our survey. Almost all cached forbs at each site were different from those cached at other sites. Pikas were exposed to a large diversity of plant communities, represented by the variation in common plants present in the environment between sites. Within the plant characteristics we analyzed, pikas selected higher quality foods than were common in the surrounding environment in almost all cases (Fig. 2). Pikas therefore exhibited both inter-site generalist behavior and intra-site selective caching behavior.

Pika populations that were provided higher quality available vegetation (with respect to nitrogen content) showed a lower degree of selectivity than populations with low quality available vegetation. This result would be expected for long-term foraging optimization (Craig et al., 1979; Katz, 1974), as pikas living in areas with predominantly low-N (and therefore low-protein) plants are more likely to supplement their cache with higher energy foods. Because of the energetic costs of haying, pikas with adequately nutritious foods readily available would not be expected to expend excess energy seeking out more nutritious and perhaps less common plants (Huntly et al., 1986).

Along with the quality of available vegetation, environmental

TABLE 1

Selectivity indices (*I*) of nutritional factors by site and environmental variables. A positive value for *I* represents selective caching for higher values of the given nutritional factor than found in available vegetation; a negative value for *I* represents selective caching for lower values of the given nutritional factor than found in available vegetation. Zero is the expected value given no selectivity. Sites are listed alphabetically.

Site	Latitude (°)	Elevation (m)	Average summer temperature (°C)	Average annual precipitation (mm)	Selectivity index (*I*) Water content	Nitrogen
Bridger Peak	41.187	3341	9.14	1392	0.033	0.213
Brown's Peak	41.352	3045	13.00	891	0.156	0.917
Crystal Lake	38.049	3593	12.13	638	0.076	0.087
Deep Lake	39.775	3221	11.27	1106	0.150	0.314
Del Norte Peak	37.593	3602	8.26	851	0.052	0.053
Grand Mesa	39.064	3099	10.29	832	0.013	0.180
Lime Creek	37.742	3057	10.12	977	0.079	0.011
Mt. Gothic	38.964	3519	7.36	965	0.027	−0.003
Nambe Lake	35.795	3717	10.90	947	0.009	0.071
Pagoda Peak	40.139	3366	11.39	1094	0.024	0.053
Silver Lake	41.309	3161	8.25	1211	0.082	−0.004
Trap Lake	40.558	3036	NA	1125	0.143	0.471
Wolf Creek Pass	37.484	3062	11.96	1130	0.127	0.386

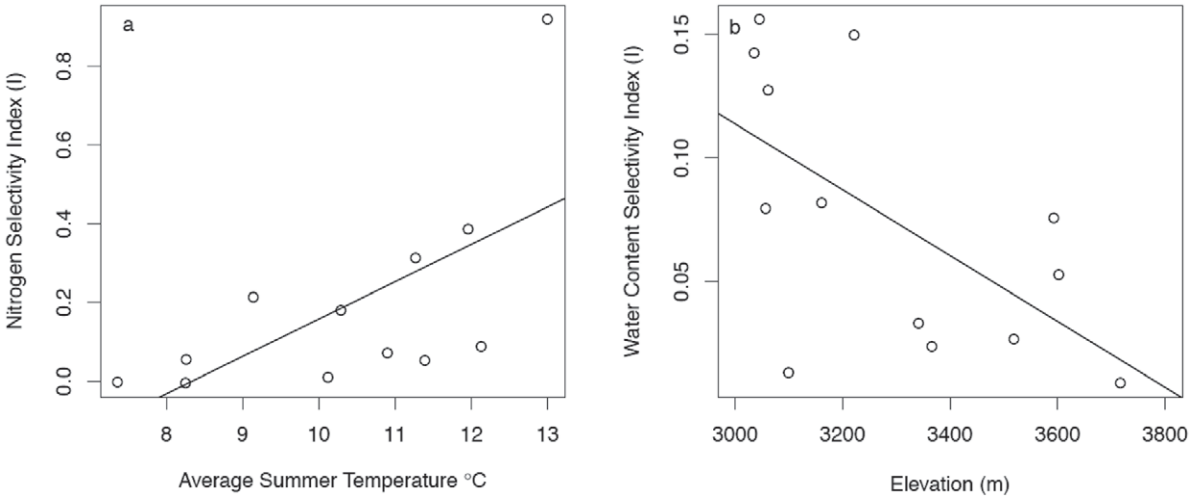

FIGURE 3. Selectivity for plants in relation to environmental variables for: (a) mean summer temperature and selectivity index for % nitrogen; and (b) elevation and selectivity index for % water content.

factors also explain variation in pika selectivity within our study area. Pikas exposed to hotter average summer temperatures demonstrated higher selectivity for nitrogen content. Given pikas' tendency to decrease daytime activity in high ambient temperatures (MacArthur and Wang, 1974; Smith, 1974), pikas may cache less forage at hotter sites. Our results suggest that some pikas are able to compensate for decreased forage quantity at hot sites by selecting vegetation of higher nutritional quality. This finding is consistent with results from both the Great Basin (Wilkening et al., 2011) and the southern Rockies (Erb, unpublished data), indicating that pika populations are more resilient to higher summer temperatures when presented with higher environmental forb availability and diversity.

Our results indicate that pikas respond differently in their selectivity for high water content. Rather than compensating for low water availability in plants, pikas were only found to selectively cache plants with high water content as elevation declined. Because water content of commonly available vegetation did not correlate with elevation, an external factor must drive this relationship. We propose that longer snow seasons and increased availability of free water at high elevations may explain this phenomenon. Low elevation sites often experience later initial snowfall and are characterized by dry late autumns in the southern Rocky Mountains. Pikas at lower elevation sites may therefore have greater need for lush forage in the autumn than do their high elevation neighbors. High elevation sites in the alpine also generally have more free water due to a higher occurrence of rock-ice features and persistent snowfields (Millar and Westfall, 2008), which act as reservoirs (Clow et al., 2003) and provide a steady influx of free water throughout the year in the form of under-talus streams (Millar and Westfall, 2010). Pikas have been reported to drink from water sources, although the frequency and importance of this behavior are unknown (C. Ray, personal communication, J. Varner, personal communication). We propose that pikas may engage in this behavior more often under the talus than is observed during surface activities, due to subsurface accumulation of water. If this is the case, a decrease in selectivity for high water content in vegetation at high elevations could be explained by higher levels of available free water for drinking.

We found that pikas responded differently to environmental conditions in selective caching behavior on the measures of food quality investigated. Selectivity for high nitrogen was related both to the quality of vegetation available and an external environmental condition, summer temperature. However, preference for high water content appeared to correlate only to an external environmental condition, elevation. Selection for plant qualities therefore appears to be contingent on different, site-specific cues and complicates our understanding of how these animals choose materials for their caches.

Acknowledgement of differential selectivity by pikas based on environmental factors may reconcile previous contradictions among studies on pikas foraging selectivity. Although the available literature on pika caching preferences is largely restricted to single-site studies, all studies combined constitute a substantially large and diverse study area when each local site is considered as part of a larger system. Our study begins to describe possible external influences on preferences for caching materials, but further research is needed to uncover the complexities that dictate patterns of selectivity across the species' range. Future studies on caching preferences of pikas should be carried out on large spatial and temporal scales and should examine a variety of plant characteristics, including nutrition, morphology, and phenolic content, in order to obtain a comprehensive understanding of the mechanisms of selectivity in this geographically widespread caching mammal.

This study provides a framework to investigate patterns of selectivity in other wide-ranging taxa, particularly those living in similarly extreme environments. Although we were unable to assess all potentially important environmental and vegetative characteristics in our system, we believe this study provides an important steppingstone in understanding how species interact with the variable environments arctic and alpine systems present. As climate change continues to alter biological systems, there is a growing need to understand how species vary their behaviors in different climatic conditions. A large-scale approach to studying foraging

behavior provides an opportunity to better understand adaptive capacity and resiliency in species that may be exposed to further environmental variability in the decades and centuries to come.

Acknowledgments

This project was funded by the University of Colorado at Boulder and the Indian Peaks Wilderness Alliance. We thank two anonymous reviewers for their constructive feedback on our manuscript. Sincere thanks to C. Ray and R. Guralnick for their invaluable contribution in providing statistical, editorial, and intellectual guidance. We thank to B. Bowman and N. Barger for providing laboratory facilities and A. Darrouzet-Nardi and S. Castle for assisting in plant sample processing and chemical analyses. We thank A. Smith and J. Benson for their editorial contributions. Finally, thanks to A. Stecker and N. Kleist for assisting in data collection.

References Cited

AOAC [Association of Official Agricultural Chemists], 1965: *Official Methods of Analysis*. 10th edition. Washington, D.C.: Association of Official Agricultural Chemists.

Bowman, W. D., Keller, A., and Nelson, M., 1999: Altitudinal variation in leaf gas exchange, nitrogen and phosphorus concentrations, and leaf mass per area in populations of *Frasera speciosa*. *Arctic, Antarctic, and Alpine Research*, 31: 191–195.

Bråthen, K. A., and Hagberg, O., 2004: More efficient estimation of plant biomass. *Journal of Vegetation Science*, 15: 653–660.

Cairns, D. M., and Malanson, G. P., 1998: Environmental variables influencing the carbon balance at the alpine treeline: a modeling approach. *Journal of Vegetation Science*, 9: 679–692.

Clow, D. W., Schrott, L., Webb, R., Campbell, D. H., Torizzo, A., and Dornblaser, M., 2003: Ground water occurrence and contributions to streamflow in an alpine catchment, Colorado Front Range. *Ground Water*, 41: 937–950.

Conner, D. A., 1983: Seasonal changes in activity pattern and the adaptive value of haying in pikas (*Ochotona princeps*). *Canadian Journal of Zoology*, 61: 411–416.

Craig, R. B., DeAngelis, D. L., and Dixon, K. R., 1979: Long- and short-term dynamic optimization models with application to the feeding strategy of the loggerhead shrike. *The American Naturalist*, 113: 31–51.

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

Gendron, R. P., and Reichman, O. J., 1995: Food perishability and inventory management: a comparison of three caching strategies. *The American Naturalist*, 145: 948–968.

Gliwicz, J., Pagacz, S., and Witczuk, J., 2006: Strategy of food plant selection in the Siberian northern pika, *Ochotona hyperborea*. *Arctic, Antarctic, and Alpine Research*, 38: 54–59.

Guisan, A., and Theurillat, J., 2000: Assessing alpine plant vulnerability to climate change: a modeling perspective. *Integrated Assessment*, 1: 307–320.

Hadj-Chikh, L. Z., Steele, M. A., and Smallwood, P. D., 1996: Caching decisions by grey squirrels: a test of the handling time and perishability hypotheses. *Animal Behaviour*, 52: 941–948.

Huntly, N. J., Smith, A. T., and Ivins, B. L., 1986: Foraging behavior of the pika (*Ochotona princeps*), with comparisons for grazing versus haying. *Journal of Mammalogy*, 67: 139–148.

Ivins, B. L., 1984: Territoriality, haypile function, and anti-predator behavior in the pika, *Ochotona princeps*. Ph.D. thesis, University of Wisconsin, Madison, Wisconsin, 177 pp.

Jonasson, S., 1988: Evaluation of the point intercept method for the estimation of plant biomass. *Oikos*, 52: 101–106.

Katz, P. L., 1974: A long-term approach to foraging optimization. *The American Naturalist*, 108: 758–782.

Körner, C., 1998: A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, 115: 445–459.

Krear, H. R., 1965: An ecological and ethological study of the pika (*Ochotona princeps saxatilis*) in the Front Range of Colorado. Ph.D. thesis, University of Colorado, Boulder, Colorado, 329 pp.

Lewis, A. R., 1982: Selection of nuts by gray squirrels and optimal foraging theory. *American Midland Naturalist*, 107: 250–257.

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

Millar, C. I., and Westfall, R. D., 2008: Rock glaciers and related periglacial landforms in the Sierra Nevada, CA, USA; inventory, distribution and climatic relationships. *Quaternary International*, 188: 90–104.

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

Millar, J. S., and Zwickel, F. C., 1972: Characteristics and ecological significance of hay piles of pikas. *Mammalia*, 36: 657–667.

Montgomery, D. C., Peck, E. A., and Vining, G., 2012: *Introduction to Linear Regression*. Hoboken, New Jersey: John Wiley & Sons, Inc., 645 pp.

PRISM Climate Group, 2010: Gridded climate data for the contiguous USA. http://prism.oregonstate.edu.

Roach, W. J., Huntly, N. J., and Inouye, R., 2001: Talus fragmentation mitigates the effects of pikas, *Ochotona princeps*, on high alpine meadows. *Oikos*, 92: 315–324.

Schwartz, M. D., and Caprio, J. M., 2003: North American first leaf and first bloom lilac phenology data. *In IGBP PAGES/World Data Center for Paleoclimatology Data Contribution Series #2003-078*. Boulder, Colorado: NOAA/NGDC Paleoclimatology Program.

Smith, A. T., 1974: The distribution and dispersal of pikas: influences of behavior and climate. *Ecology,* 55: 1368–1376.

Smith, A. T., and Weston, M. L., 1990: *Ochotona princeps*. *Mammalian Species*, 352: 1–8.

Smith, C. C., and Reichman, O. J., 1984: The evolution of food caching by birds and mammals. *Annual Review of Ecology and Systematics*, 15: 329–351.

Torregrossa, A., and Dearing, M. D., 2009: Caching as a behavioral mechanism to reduce toxin intake. *Journal of Mammalogy*, 90: 803–810.

Weber, W. A., 1976: *Rocky Mountain Flora*. Niwot, Colorado: University Press of Colorado, 359 pp.

West, E., 1980: Adaptive patterns in behavior of the Sierran pika, *Ochotona princeps*. Ph.D. thesis, University of California, Davis, California, 98 pp.

Wilkening, N. L., Ray, C., Beever, E. A., and Brussard, P. F., 2011: Modeling contemporary range retraction in Great Basin pikas (*Ochotona princeps*) using data on microclimate and microhabitat. *Quaternary International*, 235: 77–88.

MS accepted March 2013

Appendix

List of sites and top three available and cached plants with associated nutritional values. % WC = percent water content and %N = percent nitrogen. Species 1, 2, and 3 are in order of abundance of either cached or available vegetation at a site. Sites are listed alphabetically.

TABLE A1

Cached vegetation.

Site	Species 1	% WC	% N	Species 2	% WC	% N	Species 3	% WC	% N
Bridger Peak	Graminoid spp.	59.4	2.53	*Achillea lanulosa*	70.5	2.82	*Sibbaldia procumbens*	66.1	2.39
Brown's Peak	Graminoid spp.	59.5	1.77	*Lupines argenteus*	79.4	4.08	*Populus tremuloides*	61.8	1.59
Crystal Lake	Graminoid spp.	55.9	1.27	*Erigeron ursinus*	76.2	1.71	*Aquilegia saximontana*	75.5	3.00
Deep Lake	Graminoid spp.	59.7	1.86	*Thalicterum fendleri*	74.1	2.06	*Lathyrus eucosmus*	74.8	3.36
Del Norte Peak	Graminoid spp.	69.4	2.79	*Acomastylis rossii*	73.8	2.45	*Mertensia alpina*	85.0	3.52
Grand Mesa	*Aquilegia caerulea*	78.7	2.91	*Vaccinium myrtillus*	69.4	2.17	Graminoid spp.	64.9	2.00
Lime Creek	*Lonicera involucrate*	72.3	2.37	*Valeriana edulis*	83.5	2.19	*Actaea rubra*	79.2	3.53
Mt. Gothic	Graminoid spp.	63.2	2.66	*Acomastylis rossii*	67.7	2.71	*Castilleja occidentalis*	73.9	1.82
Nambe Lake	*Acomastylis rossii*	73.7	2.37	Graminoid spp.	70.9	2.40	*Pentaphylloides floribunda*	61.2	2.19
Pagoda Peak	Graminoid spp.	58.3	1.58	*Cirsium vulgare*	80.3	2.47	*Ribes montigenum*	64.9	2.20
Silver Lake	Graminoid spp.	82.3	2.69	*Erigeron flagellaris*	85.2	2.86	*Erythronium grandiflorum*	88.1	1.72
Trap Lake	Graminoid spp.	60.3	1.49	*Mertensia ciliate*	83.6	2.44	*Vaccimium scoparium*	55.5	1.64
Wolf Creek Pass	*Lonicera involucrate*	76.0	2.47	*Senecio wootonii*	86.6	2.44	Graminoid spp.	60.9	1.55

TABLE A2

Available vegetation.

Site	Species 1	% WC	% N	Species 2	% WC	% N	Species 3	% WC	% N
Bridger Peak	Graminoid spp.	59.4	2.53	*Abies lasiocarpa*	62.9	1.45	*Vaccimium scoparium*	58.5	1.88
Brown's Peak	Graminoid spp.	59.5	1.77	*Juniperus communis*	59.6	1.13	*Populus tremuloides*	61.8	1.59
Crystal Lake	Graminoid spp.	55.9	1.27	*Oreoxis alpina*	69.5	2.08	*Aquilegia saximontana*	75.5	3.00
Deep Lake	Graminoid spp.	59.7	1.86	*Paxistima myrsinites*	55.7	1.10	*Thalicterum fendleri*	74.1	2.06
Del Norte Peak	Graminoid spp.	69.4	2.79	*Acomastylis rossii*	73.8	2.45	*Pentaphylloides floribunda*	62.5	2.24
Grand Mesa	*Arnica cordifolia*	85.4	2.17	Graminoid spp.	64.9	2.00	*Ribes wolfii*	70.4	2.49
Lime Creek	*Salix planifolia*	67.6	2.58	Graminoid spp.	70.5	1.77	*Ribes inerme*	72.2	2.36
Mt. Gothic	Graminoid spp.	63.2	2.66	*Acomastylis rossii*	67.7	2.71	*Sibbaldia procumbens*	64.0	2.34
Nambe Lake	Graminoid spp.	70.9	2.40	*Acomastylis rossii*	73.7	2.37	*Saxifrage bronchialis*	70.1	1.02
Pagoda Peak	Graminoid spp.	58.3	1.58	*Juniperus communis*	57.1	1.34	*Ribes montigenum*	64.9	2.20
Silver Lake	Graminoid spp.	82.3	2.69	*Vaccimium scoparium*	61.5	2.11	*Arnica mollis*	80.6	2.81
Trap Lake	Graminoid spp.	60.3	1.49	*Abies lasiocarpa*	52.2	0.85	*Picea pungens*	55.5	0.99
Wolf Creek Pass	Graminoid spp.	60.9	1.55	*Arnica cordifolia*	85.1	1.93	*Vaccinium myrtillus*	64.8	1.80