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## Disparate determinants of summer and winter diet selection of a generalist herbivore, *Ochotona princeps*

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**Abstract** The North American pika, *Ochotona princeps*, is a generalist herbivore that simultaneously selects two distinct diets: one consumed immediately (summer diet), the other harvested, transported, and stored for later consumption (winter diet). I investigated factors influencing diet selection at two sites on the West Knoll of Niwot Ridge, Boulder County, Colorado during 1991 and 1992. The composition of summer and winter diets differed significantly from each other as well as from the relative abundance of food items in the environment. Thus, pikas were not foraging randomly for either diet. To explore winter and summer diet selection, I tested two existing hypotheses: (1) that plant morphology restricts the winter diet breadth to plants that are easily harvested and large, and thereby maximizes the amount collected per foraging effort, or (2) to compensate for nutrients lost during storage, pikas bias their winter diet with high-nutrient species. I also tested the hypothesis that plant secondary compounds may be higher in the winter diet either because they function as preservatives or because pikas delay consumption of these species until the toxins degrade. For individual dietary items, I measured energy, nitrogen, water, fiber, total phenolic, condensed tannin, and astringency contents. There was little evidence to suggest that morphology excluded plants from the winter diet. Plant size was not a good predictor of abundance in the winter diet. Even after harvesting costs had been experimentally removed, cushion plants were still not included in the winter diet. There was weak support for an effect of nutrients on winter diet selection: in three of four cases, the winter diet was significantly lower in water and higher in total energy content as predicted by the nutrient compensation hypothesis. However, other nutrients exhibited no consistent pat-

tern. Nutrients were not reliable predictors of the winter diet in multiple regression analyses. There was strong support for the hypothesis of manipulation of secondary compounds. The winter diet was significantly higher in total phenolics and astringency. Total phenolics were consistent predictors of the winter diet in multiple regression analyses. The winter diets of six additional pika populations contained plant species high in secondary compounds. The results suggest that pikas preferentially select plants with high levels of secondary compounds for their winter diet, possibly because the presence of such compounds promotes preservation of the cache. This behavior may also enable the exploitation of an otherwise unusable food resource, i.e., toxic plants.

**Key words** Diet selection · Herbivory · Nutrients · *Ochotona princeps* · Phenolics

### Introduction

Understanding the foraging behavior of an animal is central to an understanding of its ecology. Of the several abiotic and biotic factors that can influence food choice, food quality is one of paramount importance. In cases where diet quality can be effectively described by a single component, typically energy, diets can be predicted using optimal-foraging theory (Emlen 1966; MacArthur and Pianka 1966; Charnov 1976a, b; E.L. Charnov and G.H. Orians, unpublished work). Optimality theory has produced numerous successes predicting the diets of carnivorous, insectivorous, and nectivorous organisms, but has been less effective in explaining the diets of herbivores (Stephens and Krebs 1986; but see Belovsky 1978, 1981, 1984; Marken Lichtenbelt 1993). This discrepancy is most likely because in foods derived from animals, energy is positively correlated with other essential dietary components, e.g., nitrogen, while in plant foods, energy is less correlated with other nutritional variables (Stephens and Krebs 1986; Dearing and Schall 1992).

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In terms of overall food quality, plants generally appear to be more variable than animals. Nutritional contents can vary substantially both interspecifically and intraspecifically, as well as among leaves of different ages on the same individual (Coley 1983; Dearing and Schall 1992). Nutritional quality is confounded to an even greater degree by the myriad of potentially toxic secondary compounds produced by plants (Palo and Robbins 1991; Rosenthal and Berenbaum 1991, 1992). Although there have been numerous studies on the impact of either nutrients (e.g., Goldberg et al. 1980; Randolph et al. 1991; Willig and Lacher 1991; Weckerly 1994) or secondary compounds (e.g., Schwartz et al. 1980; Wrangham and Waterman 1981; Tahvanainen et al. 1985; Balanger and Bergeron 1986; Meyer and Karasov 1989) on the diet selection of mammalian herbivores, far fewer studies have simultaneously investigated both (e.g., Milton 1979; Cooper et al. 1988; Ganzhorn 1988; Marquis and Batzli 1989).

An ideal organism for exploring determinants of herbivore diet quality and their effect on diet selection is the North American pika, *Ochotona princeps* (Lagomorpha: Ochotonidae), a small generalist herbivore of alpine meadows. Analogous to other herbivores which inhabit climatically variable environments, pikas possess two seasonally distinct diets. However, pikas are peculiar in that they concurrently select these two diets from the same standing vegetation. The winter diet is harvested, transported, and stored in caches, "haypiles", underneath rocks for winter consumption, while the summer diet is consumed immediately in the meadow during the summer (Huntly et al. 1986). The ability to observe an animal simultaneously making different foraging decisions represents a unique opportunity to examine factors governing diet selection. Additionally, some of the effects of plant secondary compounds on pikas have been described (Dearing 1995).

Two hypotheses have been proposed to explain these distinct summer and winter diet preferences by pikas (Huntly et al. 1986). While gathering vegetation for their winter diet, pikas incur harvesting and transportation costs, which are negligible for the summer diet. These additional expenditures incurred during foraging for the winter diet may force pikas to avoid collecting plants that are difficult to harvest or that offer a small return per foraging effort, i.e., species of small stature. Pikas foraging for their winter diet were predicted to ignore, in particular, those species exhibiting cushion plant morphology, i.e., recumbent growth, small leaves, and underground stems (Huntly et al. 1986). This growth form may make cushion plants more difficult to harvest as well as providing less of a return than noncushion plants. Thus, differences in winter and summer diet selection may be driven by plant morphology (Huntly et al. 1986). In conjunction with or as an alternative to plant morphology, pikas may discriminate between the summer and winter diet on the basis of plant nutritional content. In some habitats, the winter diet may be stored for up to 10 months prior to consumption, and pikas may thus miti-

gate effects of nutritional decay by selecting species initially high in nutrients or species whose nutrients persist longer during storage (Huntly et al. 1986). The latter strategy, known as the perishability hypothesis, has been proposed for food-storers in general (Reichman 1988). Evidence from the literature has been used to support both the plant morphology and the nutrient compensation hypotheses (Millar and Zwickel 1972; West 1980; Huntly et al. 1986); however, neither hypothesis has been tested experimentally.

Overlooked but plausibly influential players in this scenario are plant secondary compounds. I suggest that pikas may differentiate between their summer and winter diets on the basis of the levels of secondary compounds. Furthermore, diet selection may be more sophisticated than just avoidance of plant secondary compounds (Free-land and Janzen 1974). As food-hoarders, pikas have the opportunity to gainfully manipulate secondary compounds as preservatives, thereby reducing loss to decomposition. In addition, pikas may circumvent potentially toxic effects by storing plants until toxins degrade to tolerable concentrations.

The objective of this study was to test the plant morphology, nutrient compensation, and plant secondary compound hypotheses by assessing the relative importance of plant morphology, nutrients, and plant secondary compounds to summer and winter diet selection. I documented the winter and summer diets of two subpopulations of pikas over two seasons and assessed their nutritional, morphological, and secondary compound characteristics. In addition, I investigated plant secondary compound contents of winter diets from six other pika populations occupying different habitats. I argue that pikas, as food-storing animals, have the opportunity not only to circumvent toxins behaviorally through storage, but also to exploit them.

## Materials and methods

### Study animal and study site

The North American pika (*O. princeps*; Lagomorpha) is a small (165 g), generalist herbivore common to high alpine areas in western North America (Broadbrooks 1965; Hafner and Sullivan 1995). North American pikas are not known to excavate and therefore are restricted to areas with extensive rocky outcrops where they use runways between rocks as retreats. Pikas do not hibernate and survive the alpine vegetationless period by foraging on stored vegetation ("haypile"). The haypile of one animal weighs on average 25 kg wet weight (Dearing 1995) and its construction represents a significant fraction of summer activity (Conner 1983).

Pikas were observed during July and August of 1991 and 1992 at two sites on the West Knoll of Niwot Ridge (40°03'N, 105°36'W), Nederland, Colorado. Talus cover on the West Knoll forms a roughly checkerboard pattern across the east face of the slope providing extensive pika habitat in rock islands surrounded by vegetation. The size of the pika population of the West Knoll has been estimated at 36 individuals and does not fluctuate greatly over time (Southwick et al. 1986). Site 1 was located on the lower northeast face at an elevation of approximately 3475 m, while site 2 was on the upper southeast face, at an elevation of approximately 3550 m. The shortest distance between the two sites was ap-

proximately 250 m. Dominant plant species at these sites were *Silene acaulis*, *Acomastix rossii*, *Deschampsia caespitosa*, and *Carex* species. Vegetation begins to appear immediately following the snowmelt in late June to early July and begins to senesce in mid-August (personal observation). Vegetation abundance was estimated as percent cover in 25 × 25 cm frames. Plant community structure can vary tremendously across short distances in alpine tundra (Walker et al. 1994) and pika foraging behavior can also influence plant composition (Huntly 1987). Therefore, at each site, a minimum of six quadrats at each of four distances from the talus edge (edge, 2, 4, and 6 m) was used to estimate the relative abundance of food items. Flowers and leaves of the same species were recorded as distinct food items.

### Foraging behavior

Winter and summer diets were estimated from direct observations of pikas collecting and consuming vegetation at the two sites. Pikas appeared to be undisturbed by stationary observers. To facilitate observations in the irregular habitat of the talus, I conducted all observations from either a 1-m or 2-m ladder. Using 10 × 40 binoculars, it was possible to determine the plant species consumed or collected and to estimate the number of each item. I further distinguished between the flowers, pedicels, and leaves within a species. Diet biomasses were estimated by tallying the number of each food type consumed (or collected) per pika per summer and multiplying this by the wet weight of the food type. Proportions of individual food items by wet weight were then calculated per pika, and used to calculate the means of each diet at each site and in each year. Winter and summer diet differences were evaluated using chi-square analysis. Summer and winter diets were also compared to the relative abundance of plants in the environment as estimated from the percent cover data. To control for multiple comparisons, *P*-values were adjusted by dividing alpha at 0.05 by the total number of comparisons (3).

Pikas may forage at different distances when haying than when eating (Huntly et al. 1986). Therefore, I estimated the approximate distance pikas foraged from the talus edge for both diets in 1991 and 1992. Pika foraging distances for summer and winter diets were compared using paired *t*-tests.

### Nutritional analyses of diets

I conducted several assays of the nutritional content and secondary compounds of individual food types to determine overall diet qualities. To minimize effects of individual variation within food types, several samples of each food type were combined for the assays. All results are expressed as wet weights. Total energy (Microcalorimeter Parr model 1261), fiber [cellulose and lignin combined, Acid Detergent Fiber Analysis (Van Soest 1963; Goering and Van Soest 1970)], and nitrogen (CHN Elemental Analyzer Perkin Elmer model 2400) contents were measured on dry, ground (Wiley Mill no. 20 mesh) plant material.

A literature survey suggested that phenolics were the most probable class of secondary compounds produced by plant species at the study site (Gibbs 1974). Other classes of compounds, i.e., alkaloids and cyanogenic glycosides, have not been noted for the study species (Gibbs 1974). An alkaloid spot test (Schall and Reszel 1991) confirmed data from the literature – as no species tested strongly for alkaloids. Terpenes were reported for only one species (*Artemisia scopulorum*), and no other species exhibited the characteristic monoterpene odor (Gibbs 1974; Gershenzon and Croteau 1991). Given the abiotic conditions of Niwot Ridge, i.e., limited nutrient availability coupled with high solar radiation (Bowman et al. 1993), plants are predicted to produce carbon-based compounds like phenolics (Coley et al. 1985). Therefore, I concentrated my assays of secondary compounds on phenolics.

For all phenolic analyses, plants were placed on dry ice immediately after harvest and later stored at -70°C. Phenolics were extracted in 85% MeOH using methods described in Torti et al.

(1995). Total phenolics (Folin and Ciocalteu assay in Waterman and Mole 1994), condensed tannins (Porter et al. 1986), and astringency (Hagerman and Butler 1978) were measured on all samples. Tannic acid was used as the standard in the total phenolic assay, quebracho standards were used in the condensed tannin and astringency assays. Results are expressed in milligrams of standard per gram wet weight of diet.

The amount of plant energy available to a herbivore is contingent on the fiber and secondary compound contents of the plant. Because neither the energy in fiber, nor that in many secondary compounds is easily digestible, available energy decreases as these contributions to the total energy content increase (Robbins 1993). To compare the available energy contents of summer and winter diets, I derived crude estimates by deducting the amount of energy contained in the phenolic and fiber fractions from the total energy content. The energy contained in phenolic and fiber fractions was calculated from their proportions in the diet, multiplied by their caloric contents. Proportions of phenolics and fiber in the diets were based on the total phenolic and cellulose/lignin assays, respectively, described above. Caloric contents of fiber and phenolics were estimated from the literature (Weast et al. 1987; Williams et al. 1987; Pearcy et al. 1989). To account for differing caloric values of fiber components, the caloric content of fiber (4.983 kcal/g) used here was based on a 36% lignin to 64% cellulose fiber ratio, determined from cellulose and lignin assays (Van Soest 1963; Goering and Van Soest 1970) performed on eight species from the study site. For phenolic energy content, I used the energy value of a representative hydrolyzable tannin, pentagalloyl-glucose (3.725 kcal/g), because preliminary analyses suggested that hydrolyzable tannins were the most common phenolics in the food plants.

Food types comprising less than 2% of both diet and percent cover at a site were considered insignificant and were excluded from the analyses. By this accounting, the total biomass described for each diet ranged from 90 to 99%. To compensate for these differences between diets, I standardized diets by dividing the total wet weight accounted for in each diet by the wet weight of each food type included in the analysis. To estimate the total dietary concentration of any one nutritional or phenolic variable, the standardized food item proportion was multiplied by the nutritional variable of interest for that food type. Nutritional contributions of individual food types were then summed to provide an overall estimate of each nutrient or phenolic assay per diet. These calculations were performed for the summer and winter diet of individual pikas. All animals included in this analysis were observed for a minimum of five times per diet, per season. Differences in plant quality among diets were assessed with either a *t*-test or Wilcoxon sign rank test, depending on whether the variables had normal distributions.

### Diet selection

To determine whether pikas avoided collecting cushion plants for their winter diet as predicted by the plant morphology hypothesis, I conducted a field experiment in 1991 with *S. acaulis*, a cushion plant common in the summer diet. Cushion plants are mat-forming, prostrate species that share common woody stems (Huntly et al. 1986). Because of the inaccessibility of the woody stems, this growth form may require more harvesting effort than forbs that are not cushion plants and, therefore, cushion plants may not be as common in the winter diet. Portions of *S. acaulis* were harvested and placed in water-filled florist tubes that had been inserted into the meadow within 1 m of the talus edge. As a positive control, I simultaneously placed approximately equivalent amounts of *A. rossii* leaves in an adjacent (within 5 cm) tube; preliminary data had suggested that *A. rossii* was common in winter diets. I observed the behavior of pikas at the experimental stations containing harvested vegetation, for up to 4 h. To obtain sufficient observations from a number of pikas, this experiment was conducted over 8 days. At the beginning of each day, any vegetation remaining from previous days was replaced with fresh vegetation.

To determine which of the independent variables (dry weight, nitrogen, energy, fiber, total phenolics, condensed tannins, astringency, plant relative abundance, plant size) were useful in predicting abundance of food types in the diet, I performed stepwise multiple regressions for each site, year, and diet. Nitrogen, energy, fiber, total phenolics, condensed tannins, and astringency were expressed in dry weight per gram of food type. Plant size was the average wet weight ( $n = 10$ ) of the total leaves or flowers on an individual. Prior to the stepwise analysis, all variables were checked for normality. Several of the potential variables exhibited nonnormal distributions and required transformation prior to the analyses. Percent cover, condensed tannins, and total phenolics were transformed to normal distributions by  $\log_{10}(\text{variable} + 1)$ . Plant size was transformed using  $\ln(\text{variable} + 1)$ . The dependent variable was also nonnormally distributed but could not be transformed otherwise using standard transformation functions. All other variables were considered normally distributed (Shapiro and Wilk 1965).

Several significant correlations among the independent variables were suggestive of potential multicollinearities (Glantz and Slinker 1990). To reduce redundant information in the preliminary stepwise analyses, astringency and percent dry weight were removed because they were significantly correlated with other independent variables but were not significantly correlated with the dependent variable (abundance in the diet).

#### Secondary compounds of other pika haypiles

To determine whether pikas in other habitats collected plants with high levels of secondary compounds, in August 1993, I collected pika haypiles from two other study sites with differing floras. One site was also located on Niwot Ridge, approximately 1.5 km southeast of the primary study site and at a lower elevation, approximately 3300 m. This site was at the upper limits of the tree line. The talus was surrounded by limber pine, *Pinus flexilis*, and willow (*Salix* species). Shrubby cinquefoil, *Pentstemon floribunda*, predominated within the talus. The other site was located on Campito Mountain (51°N, 118°W) in the White Mountains near Bishop, California. The elevation was approximately 3000 m and the climate was considerably drier than in either of the Colorado sites. Sagebrush, *Artemisia tridentata*, comprised most of the phytomass.

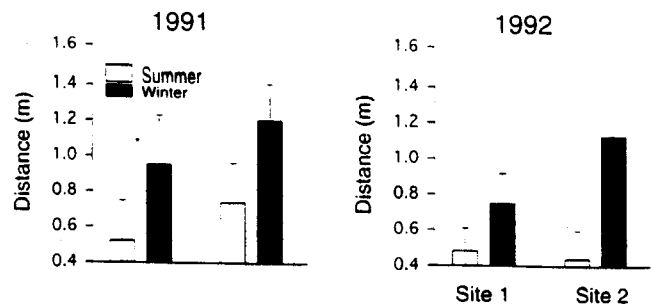
At each of these sites, I collected approximately 100-g samples from five pika haypiles. Haypile contents were oven dried at 40°C and sorted to species. I collected fresh samples of all common vegetation in the habitat for phenolic analyses. These samples were stored at -70°C and analyzed for total phenolics as described above.

To further examine the contents of secondary compounds in other pika haypiles, I surveyed the literature on the secondary chemistry of plant species found in pika haypiles, and found three reports in the literature on the contents of *O. princeps* haypiles. Two studies listed plant species occurring in haypiles by percent of the total dry weight (Millar and Zwickel 1972; Elliott 1980), while the third was a qualitative assessment (Broadbrooks 1965). In the latter, the results were reported only for species described as common in haypiles. There was also a quantitative report of the haypile contents of the Japanese pika, *Ochotona hyberborea*; however, the sample size was one haypile (Haga 1960). The two primary sources for plant secondary chemistry were Duke (1985) and Glasby (1991).

## Results

### Foraging distances

At both sites and in both years, pikas foraged for their summer and winter diets within 1.3 m of the talus edge (Fig. 1). Pikas tended to forage at least twice as far from



**Fig. 1** The mean distances pikas foraged from the talus for their summer and winter diets. Error bars are 1 SE and asterisks represent significance at  $P = 0.05$ . Summed sample sizes of haying and eating observations in 1991 were 313 observations of seven pikas at site 1 and 192 observations of five pikas at site 2; in 1992, 353 observations of five pikas at site 1 and 2333 observations of nine pikas at site 2

the talus edge for their winter than for their summer diets. However, there was tremendous variation in grazing and haying distances and, hence, at only one site and in one year were the differences statistically significant. Because pikas consumed or collected vegetation within 2 m of the talus, and because the relative abundance of plants at the edge and at 2 m were similar, the relative abundance of available vegetation was estimated by combining the edge and 2-m samples.

### Composition of summer and winter diets

Over both seasons and sites, a total of 26 pikas were observed foraging for either diet a minimum of five times. Twenty of these animals met the five-observations minimum for both diets per season. Over the two summers of the study, I observed 2106 cases of pikas consuming or collecting vegetation. Pikas spend considerably more time collecting vegetation than consuming it; this resulted in more observations of individuals collecting the winter diet than consuming the summer diet (Table 1).

Pikas did not forage randomly for either their summer or winter diet. Over both sites and years, winter and summer diets differed both from plant relative abundance and from each other (Table 2, Fig. 2). Pikas foraged as generalists for their summer diets, consuming several plant species with no single species comprising more than 50% of the diet. Plant species common in the summer diets (10–30% of wet weight) were *Trifolium parryi* leaves, *S. acaulis* leaves, *A. rossii* leaves, graminoids, and *Bistorta bistortoides* leaves and flower heads. Of these, *T. parryi* comprised a larger proportion of the diet than expected from its relative abundance: *S. acaulis* and *B. bistortoides* were taken in proportion to their relative abundance; grasses and *A. rossii* were consumed less frequently than their relative abundance. Species prevalent in the summer diets varied moderately among sites with respect to diet inclusion. *T. parryi* leaves were most common at site 1 in both years, and site 2 in 1992. However, at site 2 in 1991, *S. acaulis* was the most common food type.

**Table 1** Number of observations of pikas consuming or collecting vegetation at each site and in each year. At site 1 in 1992, two of six pikas had been observed in 1991; at site 2 in 1992, six of 11 pikas had been observed during the previous summer

	1991		1992	
	Summer	Winter	Summer	Winter
Site 1				
Mean (SE) number of observations per pika	28.7 (4.5)	73.4 (13.1)	20.8 (2.1)	52.5 (12.1)
Total number of observations	201	603	104	315
Number of pikas	7	8	5	6
Site 2				
Mean (SE) number of observations per pika	16 (2.9)	30.7 (13.8)	8.7 (1.2)	37
Total number of observations	112	277	87	407
Number of pikas	7	10	10	11

**Table 2** Chi-square comparisons of proportions of food types in the summer and winter diets and the environment. To compensate for multiple comparisons, the significance level was reduced to  $P = 0.017$ . All comparisons are significant at  $P = 0.005$  (RA relative abundance in the environment). df = number of food types - 1

R	Summer vs. RA		Winter vs. RA		Summer vs Winter	
	$\chi^2$	df	$\chi^2$	df	$\chi^2$	df
1991 site 1	228	14	87	14	368	11
1991 site 2	130	14	30	14	513	11
1992 site 1	273	14	88	14	984	9
1992 site 2	64	13	263	13	392	10

Pikas were much more specialized with respect to their winter diet selection. At both sites and in both years, *A. rossii* leaves comprised on average 60–77% of the winter diet, far more than would be expected from its relative abundance (Fig. 2), and departing significantly from its use in the summer diet where it was taken far below its relative abundance. No other food items at either site comprised more than 13% of the winter diet; most comprised less than 10%. In the 5–13% category were *B. bistortoides* flowers and leaves, graminoids, and *T. parryi*.

#### Harvested-vegetation experiment

Harvesting costs had little impact on the inclusion of cushion plants (*S. acaulis*) in the winter diet. Eleven pikas collected vegetation from the experimental stations containing harvested vegetation. Pikas simultaneously collected the harvested *A. rossii* and *S. acaulis* leaves eight times. In 47 observations, pikas collected only one of the two choices. In these cases, *A. rossii* leaves were collected significantly more frequently ( $n = 42$ ) than *S. acaulis* leaves ( $n = 5$ ;  $\chi^2 = 29.1$ ,  $df = 1$ ,  $P < 0.05$ ).

#### Fiber, nitrogen, and energy contents

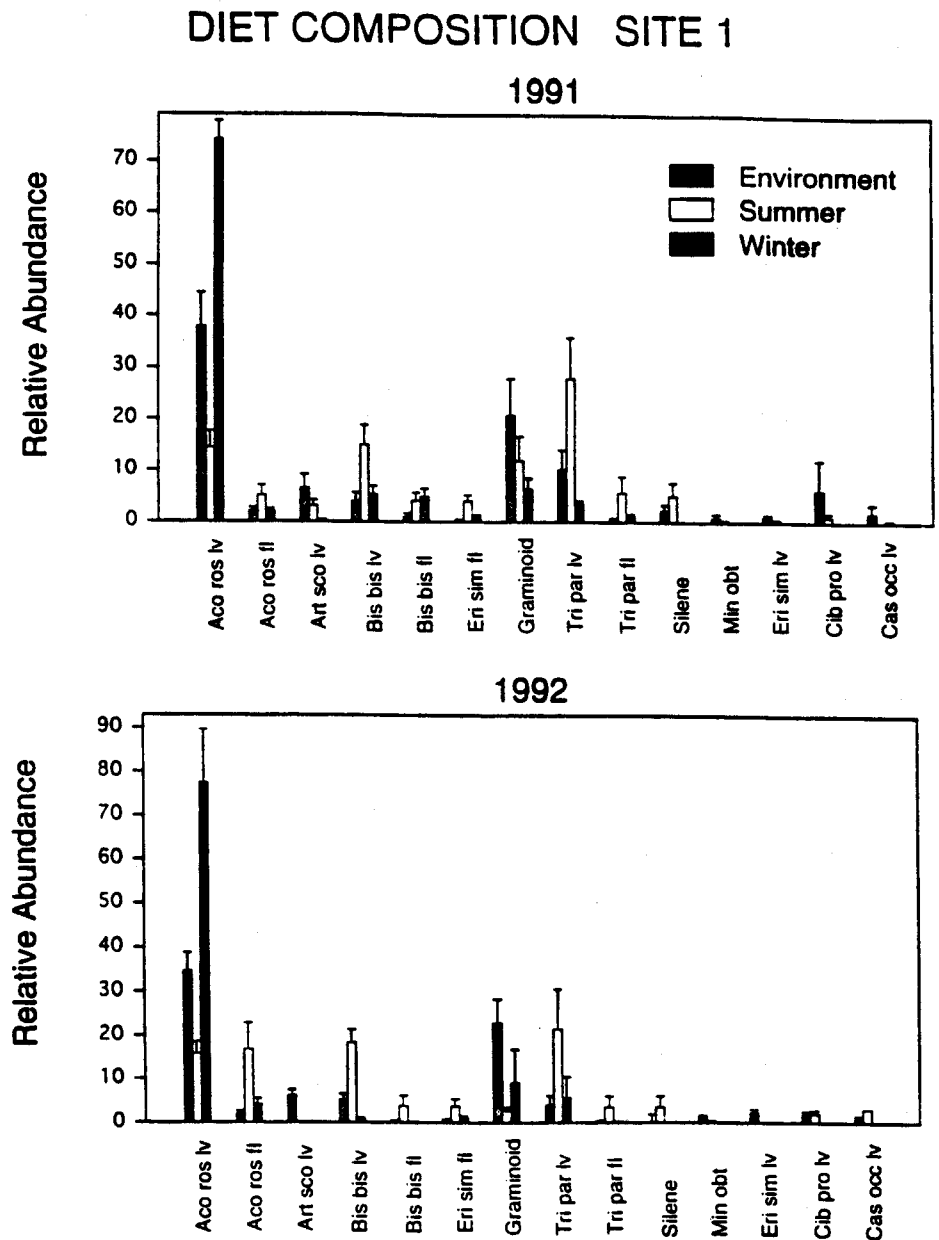
The winter and summer diets were relatively similar in overall nutritional content, and the most consistent difference was that the winter diet was lower in water content in three of the four comparisons (Table 3). Thus, the winter diet contained 3.1–17% more dry weight biomass

per wet weight collected the summer diet. Because of these differences in water content, total energy content per gram wet weight was significantly lower, approximately 10%, in the summer diet in three of four comparisons. Regardless of this disparity, there was no difference in available energy content in three of four comparisons. Nitrogen content differed significantly between summer and winter diets at both sites in 1992, but did not differ at either site in 1991. There was no particular trend in the differences: in 1992 at site 1, the winter diet was higher in nitrogen, while at site 2, the summer diet was higher in nitrogen. Fiber content was significantly higher in the summer diet in two of the four comparisons.

#### Phenolic contents

In contrast to nutrients, there were substantial and consistent differences between summer and winter diets in total phenolics and astringency (Table 4). At both sites in both years, the winter diet contained 2- to 3-fold more total phenolics than the summer diet and was 2- to 2.5-fold more astringent. Total phenolics comprised approximately one quarter of the dry weight of the winter diet. The leaves of a single species, *A. rossii*, were responsible for 91–96% of the total phenolics and astringency present in the winter diet. Interdiet differences in condensed tannin content did not parallel differences in total phenolics and astringency in magnitude or direction. Summer diets at site 1 contained significantly more condensed tannins, while there were no differences in condensed tannin levels in the diets at site 2. In both summer and winter diets, condensed tannin levels were trivial.

**Fig. 2** Relative food type abundances (%) in the environment, and in the summer and winter diets at the two sites in 1991 and 1992. Food types from left to right: *Aco ros* lv, *Acomastylis rossii* leaves; *Aco ros* fl, *A. rossii* flowers; *Art sco* lv, *Artemisia scopulorum* leaves; *Bis bis* lv, *Bistorta bistortoides* leaves; *Bis bis* fl, *B. bistortoides* flowers; *Eri sim* fl, *Erigeron simplex* flowers; Graminoid, *Carex* sp. and *Deschampsia caespitosa*; *Tri par* lv, *Trifolium parryi* leaves; *Tri par* fl, *T. parryi* flowers; *Silene*, *Silene acaulis* flowers and leaves; *Min obt*, *Minuartia obtusiloba* flowers and leaves; *Eri sim* lv, *E. simplex* leaves; *Cib pro* lv, *Cibbaldia procumbens* flowers and leaves; *Cas occ* lv, *Castilleja occidentalis* flowers and leaves. In cases where flowers were rarely abundant and rarely consumed, e.g., *Silene*, leaves and flowers were combined into one food type



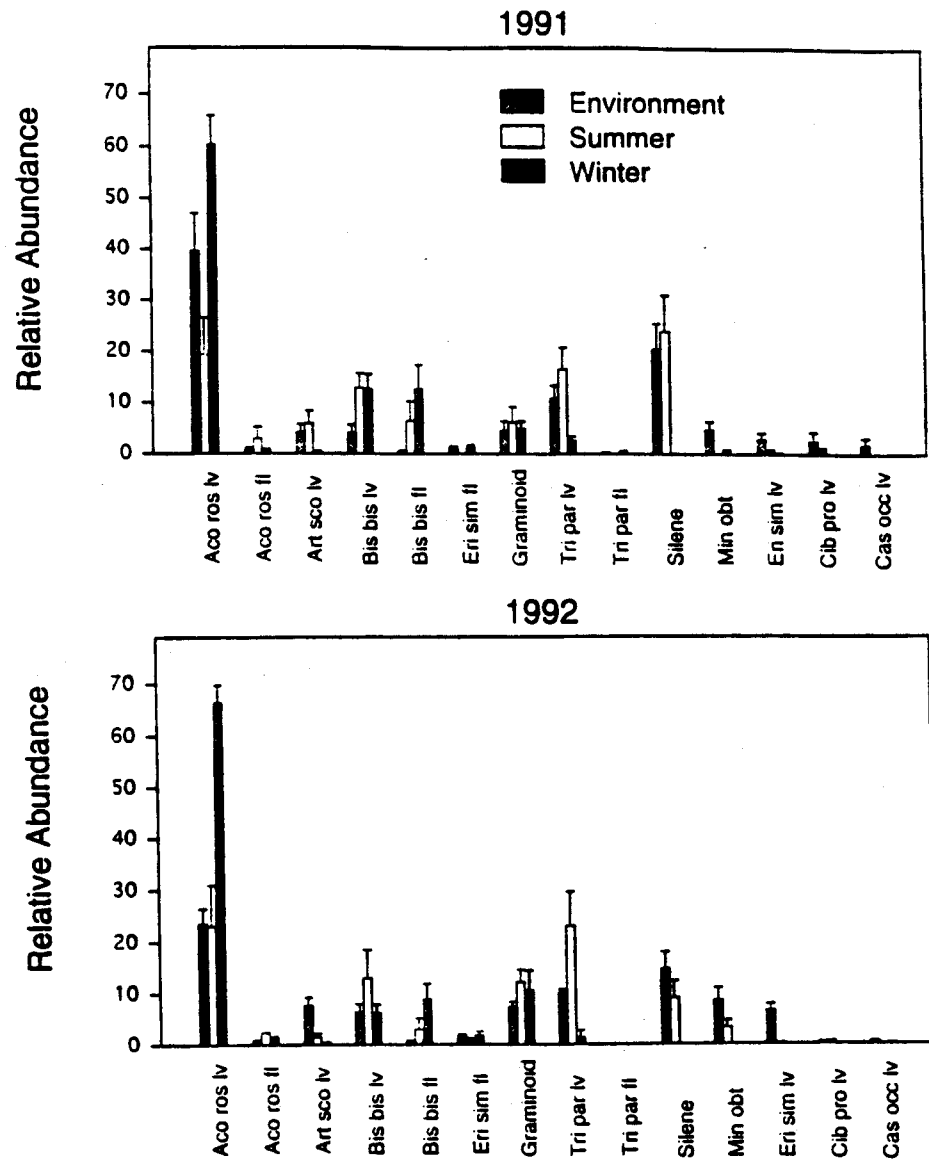
**Table 3** Mean (SE in parentheses) of nutrient contents of summer and winter diets at both Niwot Ridge sites in 1991 and 1992. Energy, nitrogen, and fiber are given in units per gram wet weight of diet. Available energy is the energy content after fiber and phenol-

ic contributions have been removed. All statistical comparisons were made between diets within the same site. Asterisks denote significance at  $P < 0.05$

	Site 1 1991		Site 2 1991		Site 1 1992		Site 2 1992	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Number of pikas	7	8	7	10	5	6	10	11
Dry Weight (%)	24.1 * (0.7)	26.2 (0.1)	24.1 * (0.3)	25.9 (0.3)	22.8 * (0.3)	26.7 (0.5)	25.9 (0.4)	26.7 (0.4)
Energy (kcal/g)	1.132 * (0.033)	1.257 (0.055)	1.212 * (0.19)	1.274 (0.19)	1.065 * (0.016)	1.212 (0.018)	1.273 (0.019)	1.283 (0.019)
Nitrogen (%)	0.79 (0.02)	0.81 (0.01)	0.79 (0.01)	0.80 (0.01)	0.74 * (0.03)	0.82 (0.02)	0.84 * (0.02)	0.81 (0.01)
Fiber (%)	6.1 * (0.4)	4.7 (0.2)	5.8 (0.2)	5.3 (0.3)	5.5 (0.2)	4.5 (0.6)	6.5 * (0.4)	5.2 (0.2)
Available energy (kcal/g)	0.736 (0.020)	0.743 (0.005)	0.747 (0.015)	0.725 (0.011)	0.676 * (0.015)	0.763 (0.029)	0.774 (0.009)	0.756 (0.016)

Fig. 2 (continued)

## DIET COMPOSITION SITE 2



**Table 4** Means (SE in parentheses) phenolic contents of the summer and winter diets at both Niwot Ridge sites in 1991 and 1992. All phenolic concentrations were calculated in mg of phenolic

equivalent per gram wet weight of diet. All statistical comparisons are for diets within the same site; asterisks denote significance at the 0.05 level or less.

	Site 1 1991		Site 2 1991		Site 1 1992		Site 2 1992	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Number of pikas	7	8	7	10	5	6	10	11
Total phenolics (mg TAE/g)	24.4 *	75.7	29.4 *	65.1	30.4 *	78.4	30.6 *	69.6
	(2.4)	(3.2)	(6.2)	(4.8)	(1.8)	(11.4)	(6.8)	(2.8)
Condensed tannins (mg QE/g)	10.2 *	4.6	10.3	11.5	13.0	0.4	8.3	6.8
	(2.1)	(1.0)	(2.7)	(2.6)	(3.0)	(0.2)	(2.7)	(1.9)
Astringency (mg QE/g)	53.5 *	123.9	47.9 *	110.4	53.5 *	123.9	47.9 *	110.4
	(3.8)	(17.8)	(10.9)	(4.4)	(3.8)	(17.8)	(10.9)	(4.3)

**Table 5** Stepwise regression analysis of independent variables (energy, nitrogen, fiber, total phenolics, condensed tannins, plant size and relative abundance) regressed on wet weight amounts of food

Summer					Winter				
	$r^2$	PE	$F$	$P$		$r^2$	PE	$F$	$P$
Site 1									
1991									
Nitrogen	0.56	7.76	12.3	0.002	Percent cover	0.42	21.5	8.5	0.01
Percent cover	0.09	5.88	2.9	0.11	Phenolics	0.12	16.8	2.9	0.12
Total	0.65		7.81	0.003	Total	0.54		6.4	0.02
1992									
Nitrogen	0.38	7.81	7.2	0.02	Percent cover	0.42	32.1	8.8	0.01
Total	0.38			0.02	Phenolics	0.18	23.8	4.8	0.05
					Nitrogen	0.11	-12.2	3.8	0.08
					Total	0.71			0.005
Site 2									
1991									
Percent cover	0.66	10.8	23.7	0.0004	Phenolics	0.33	22.1	5.8	0.03
Energy	0.16	0.02	10.0	0.009	Percent cover	0.24	19.8	5.9	0.03
Nitrogen	0.05	4.7	4.1	0.07	Energy	0.10	-0.05	2.9	0.12
Plant size	0.03	3.1	2.5	0.15	Total	0.66			0.01
Total	0.90		20.8	0.0001					
1992									
Percent cover	0.45	10.8	9.7	0.009	Phenolics	0.30	22.3	5.1	0.04
Nitrogen	0.19	6.2	5.9	0.03	Percent cover	0.21	18.3	4.5	0.06
Total	0.64		9.8	0.004	Total	0.51		5.6	0.02

comprising on average less than 3.2% of the total dry weight of the diet.

### Multiple regression analyses

The intent of the final stepwise analyses was to determine which, if any, of the independent variables were correlated with plant species abundance in the diet. Independent variables that correlate with plant abundance in the diet might be factors governing diet selection. The final analysis revealed that regardless of year or site, both the summer and winter diets were associated with their own unique set of predictor variables (Table 5). For the summer diet, nitrogen explained a significant fraction of the variation in three of four cases, and entered into the model in the fourth case. Percent cover also explained a portion of the summer diet variation. Together, nitrogen and percent cover accounted for approximately 66% of the variation in the amount of food types consumed in the summer diet. Nitrogen explained more of the variation at site 1, while percent cover was relatively more important at site 2. In one case, energy and plant size also entered into the stepwise model.

In the winter diet, total phenolics and percent cover appeared equally important as explanatory variables in diet selection, and together described on average 55% of the variation (Table 5). Total phenolics and percent cover entered the model in all cases and both contributed significantly to the model in three of the four instances. In one case, energy and nitrogen entered the model; howev-

types consumed at site 1 and 2. Variable order represents entry into the model; no variables were subsequently removed after entry into the model in any of the analyses (PE parameter estimate)

**Table 6** Total phenolic concentrations of plants in haypiles at two additional study sites, Niwot Ridge, Colorado and Campito Mountain, California. The contents of five haypiles were sampled at each site. Means of species representations in the haypile are given as percent dry weight (SE in parentheses). Asterisks denote species that contain over 6% total phenolics by dry weight

Plant species	Percent of haypile	Phenolics mg/g
<b>Niwot Ridge</b>		
Poaceae		
Graminoids	39.6 (10.5)	2.5
Rosaceae		
<i>Pentaphylloides floribunda</i> *	31.5 (9.8)	93.7
Salicaceae		
<i>Salix</i> sp.	6.1 (4.0)	2.6
Asteraceae		
<i>Cirsium</i> sp.	5.0 (3.0)	0.9
<i>Hymenoxys</i> sp.	2.5 (1.0)	3.5
<i>Campanula rotundifolia</i>		
<i>Campanula rotundifolia</i>	2.8 (2.3)	2.9
<b>Campito Mountain</b>		
Poaceae		
Graminoids	50.9 (15.0)	5.8
Asteraceae		
<i>Artemisia tridentata</i> *	19.8 (8.8)	126.7
<i>Chrysothamnus nauseosus</i>	4.5 (1.9)	12.1
Polemoniaceae		
<i>Leptodactylon pungens</i> *	14.9 (6.4)	85.4
Grossularaceae		
<i>Ribes</i> sp.	7.1	131.7

**Table 7** Common plant species and associated secondary metabolites of pika haypiles. Data were taken from the literature. Abundance is the percent abundance in the haypile, except for the Bethel Ridge data where it represents the number of haypiles sampled containing that species. CA alkaloids, AA neurotoxic amino acids, C coumarins, CA carboline alkaloids, CG cardiac glycosides, CT condensed tannins, PA pyrrolizidine alkaloids, P phenolics, QA quinolizidine alkaloids, SA steroid alkaloids, T terpenes. Specific compounds or the number of compounds in that group that have

been identified for that species/genus are given after the abbreviation. Reports of livestock poisoning are listed by plant species (S), genus (G), or family (F). Plants considered poisonous when ingested by humans, are indicated with a Y. References: a Elliott 1980, b Millar and Zwickel 1972, c Broadbrooks 1965, d Haga 1960, e Gibbs 1974, Duke 1985, Glasby 1991, Rosenthal and Berenbaum 1991; f Lewis and Elvin-Lewis 1977, Duke 1985, Rosenthal and Berenbaum 1991; g Turner and Szczawinski 1991

	Abundance	Compounds <sup>c</sup>	Livestock Poisoning <sup>f</sup>	Poisonous <sup>g</sup>
<i>Ochotona princeps</i>				
Payette National Forest, Idaho <sup>a</sup>				
<i>Smilacina stellata</i>	70.5	CG?		
<i>Apocynum adroeamifolium</i>	11.0	CG: cymar	S	Y
<i>Fragaria virginia</i>	5.8	P: quercitin, tannin acid		
Bow Forest, Colo <sup>b</sup>				
<i>Shepherdia canadensis</i>	22.0	CA, P: tannins?		
<i>Ribes</i> sp.	11.0	P: quercitin, phenol		
<i>Salix</i> sp.	6.5	P: phenolic glycosides, hydroquinone		
Bethel Ridge, WA <sup>c</sup>				
<i>Luina stricta</i>	16.0	T: sesquiterpene lactones	F	
<i>Lathyrus lanzwertii</i>	16.0	P: A: AA	G	Y
<i>Lupinus sulphureus</i>	11.0	PA: QA	G	Y
<i>Vaccinium scoparium</i>	7	IG: CT: 14: QA: C: P: benzoic acid, hydroquinone		
<i>Ochotona hyperborea</i> <sup>d</sup>				
<i>Rubeshibe, Japan</i>				
<i>Dryopteris dilatata</i>	58.5	CT: oloeresin	G	Y
<i>D. crassirhizoma</i>	17.5	CT: oloeresin	G	Y
<i>Pachysandra terminalis</i>	13.2	SA: 22: T: 10	F	Y

er, the parameter estimates were negative, suggesting that plants with lower concentrations of energy and nitrogen were included in the diet.

#### Phenolic concentrations of other pika winter diets

At both the additional Colorado and California sites, winter diets contained abundant quantities of plant species high in total phenolics, i.e., 8% dry weight (Table 6). At the Colorado site, the second most common species in the winter diet, *P. floribunda*, was nearly 10% phenolics by dry weight. At the California site, three species totaling 42% of the haypile contained phenolic concentrations ranging from 8.5 to 13.5% of the dry weight (Table 6).

The results of the secondary chemistry in winter diets of other populations of *O. princeps* and one *O. hyperborea* population are given in Table 7. A broad range of secondary compounds was represented in the 12 plant genera common in these haypiles. Several compounds, including potent cardiac glycosides, terpenes, and all major subclasses of alkaloids were considered toxicologically active. Five genera were renowned for their extreme toxicity as they have been credited for cases of livestock poisoning and are toxic when ingested by humans.

#### Discussion

Although a universal set of factors governing diet selection by generalist mammalian herbivores has not yet been described, it is commonly accepted that the foraging strategy employed by mammalian herbivores integrates nutrient preference with toxin avoidance (Palo and Robbins 1991). The selection of the summer diet by pikas exemplifies this foraging scheme. The summer diet was high in nitrogen and low in plant secondary compounds. Winter diet selection, however, appeared to be organized by a novel foraging principle as pikas selected a winter diet high in secondary compounds.

There was little support for the hypothesis that pikas choose their diets on the basis of plant morphology (Huntly et al. 1986). One prediction of the plant morphology hypothesis is that pikas should collect larger species for their winter diet to maximize the amount of vegetation collected per foraging trip. The results of the stepwise regression suggested that plant size does not explain the variation in the winter diet. Another prediction of the plant morphology hypothesis is that pikas should avoid plants that are difficult to harvest for their winter diet, especially cushion plants such as *S. acaulis*. Although cushion plants were consistently absent from the winter diet, this does not appear to be due to morphology. When presented with harvested cushion plants, pikas

still did not incorporate them in the winter diet. This implies that factors other than harvesting costs exclude cushion plants from the winter diet.

The effects of plant morphology on diet selection may be more pronounced in habitats where a large proportion of the available vegetation exhibits cushion plant morphology. At the sites on the West Knoll, cushion plants comprised at most only 15% of the cover, and use of cushion plants in the summer diet appeared to be intricately linked to availability. At site 1, where cushion plants were not very abundant, they did not comprise much of the summer diet, while at site 2, cushion plant abundance in the diet increased with plant availability (Fig. 2). Thus, absolute abundance of food types had a significant impact on their use by pikas. In cushion-plant-dominated communities, i.e., fell fields, the benefits of discriminating between cushion and noncushion plants in the winter diet may be more marked than in habitats like the West Knoll, where cushion plants are not very common.

The nutrient compensation hypothesis predicts that the winter diet should be higher in nutrients than the summer diet to offset loss to decay during storage (Huntly et al. 1986). The univariate analyses of dry weight and energy tended to support this hypothesis, since these variables were greater in the winter diet in three of four cases. The difference in energy content between the winter and summer diets was within the limits of mammalian detection; thus, it is possible that pikas are discriminating on total energy content (Post 1993; own personal observation). However, in general, nutrients were not consistent predictor variables in the stepwise regression of the winter diets. Two nutrient variables, energy and nitrogen, appeared once each as predictors of diet. Moreover, in both cases, the variables had negative parameter estimates, i.e., foods high in nutrients comprised little of the diet. This evidence is counter to the prediction of the nutrient compensation hypothesis. In contrast, there was selection for nutrient content in the summer diet, as nitrogen consistently emerged as an explanatory variable with positive parameter estimates in the stepwise regressions. Thus, high-nitrogen food types appear to be notable in summer diet preferences but less so in winter diet selection.

Data from the literature given by Huntly et al. (1986) in support of the nutrient compensation hypothesis were based on the nutrient content of individual plant species: the abundance of these items in the winter diet was not considered (Millar and Zwickel 1972). Thus, it is unclear from these studies what the actual nutritional content of the winter diet was. Moreover, the comparison cited was between available vegetation and the winter diet (Millar and Zwickel 1972), while the nutrient compensation hypothesis is based on a contrast between the summer and winter diets (Huntly et al. 1986).

The secondary compound-manipulation hypothesis predicts that concentrations of phenolics should be greater in the winter than in the summer diet. Of all variables measured in this study, phenolic concentration exhibited the most pronounced difference between the summer and

winter diets. In the stepwise analyses, total phenolics consistently explained significant amounts of the variation in the proportion of food items collected for winter diets. The winter diet was 2 to 3 fold higher in total phenolics and astringency, with more than one quarter of the dry weight consisting of phenolics. The majority of the phenolics in the winter diet were attributable to phenolic-rich and abundant *A. rossii* leaves.

It is interesting that an animal would collect a diet consisting primarily of a plant species (*A. rossii*) which is uncommon in its summer diet, contains high concentrations of phenolics, and also produces detrimental effects. Phenolics when ingested by mammalian herbivores can produce any of a spectrum of difficulties, ranging from decreased digestibility to toxicity (Hagerman and Butler 1991). In feeding trials, pikas consuming diets of 25–50% *A. rossii*, less than that found in the winter diet, showed decreased fiber, nitrogen, and dry matter digestion, and increased levels of detoxification by-products in their urine (Dearing 1995).

The collection and storage of plants with high concentrations of secondary compounds for the haypile was not confined to the West Knoll study population. In two other pika populations from different habitats, haypiles contained significant quantities of species containing high concentrations of phenolics. Moreover, at the White Mountain, California site, *A. tridentata* and *Chrysothamnus nauseosus* together comprised 25% of the haypile. Both species are noted for remarkably diverse and toxic secondary chemistries, and both have been responsible for cases of livestock poisoning (Johnson et al. 1976; Duke 1985). In addition, five of the 12 plant genera present in haypiles described in the literature survey contain compounds with potent pharmacological activity (Table 7).

One possible explanation for the unusual behavior of collecting toxic plants is that pikas may be selecting plants high in secondary compounds for their winter diet for purposes other than food. Plant phenolics and terpenes have reputable antibacterial and antifungal activities which retard decomposition (Swain 1978; Swift et al. 1979). For example, in a number of studies, leaves with high concentrations of these compounds decayed far more slowly than those with low concentrations (Anderson et al. 1978; Cameron and LaPoint 1978; Swift et al. 1979; Stout 1989). Thus, pikas may not be collecting plants rich in secondary compounds for future consumption, but rather may be exploiting their antibacterial and antifungal properties to enhance the preservation of winter diet plants lacking these compounds.

Alternatively, pikas may be selecting for their winter diet, vegetation containing high concentrations of plant secondary compounds which render the food too toxic or costly to process immediately. However, if these compounds degrade during storage to acceptable concentrations, pikas could exploit an otherwise unusable food resource and thereby expand their diet breadth.

These two hypotheses, the use of phenolic-rich plants as preservatives and the manipulation of toxic plants through storage, are not mutually exclusive and may actually function in concert. Pikas may initially store plants

because they are too toxic for consumption, and the toxins may facilitate preservation until their eventual decay. This is somewhat similar to the nutrient compensation (perishability) hypothesis (Reichman 1988), in that pikas are selecting plants that preserve the best; however, the preservation mechanism differs from anything predicted by the nutrient compensation or perishability hypothesis.

The data presented here imply that preservation may have a greater impact than toxin reduction in structuring the winter diet selection of West Knoll pikas, because pikas exhibit extreme selectivity for their winter as well as their summer diet plants. If the expansion of diet breadth through the utilization of toxic species was the primary motivation for collection of toxic plants, then all else being equal, the winter diet would be expected to be similar to plant relative availability as toxic species are added to the diet. That the majority of the winter diet consists of phenolic-rich *A. rossii*, and that *A. rossii* is collected in 2-fold excess of its availability, implies that some component of *A. rossii* renders it strongly preferred. The overall nutrient content of *A. rossii* does not seem to explain its predominance in the winter diet (Dearing 1995). It contains average levels of dry mass and energy and while it is far lower in fiber content, its digestible energy is average due to its high phenolic concentration. Nitrogen contents are slightly higher than average, but not outstanding. Therefore, it is plausible that the high phenolic concentrations of *A. rossii* confer superior preservative qualities which cause it to be strongly preferred for the winter diet.

The list of secondary compounds occurring in plants in all haypiles surveyed is impressive for a generalist herbivore. Most generalist herbivores are thought to have limited detoxification abilities (Freeland and Janzen 1974; McArthur et al. 1991). Given the detrimental effects of *A. rossii* consumption on pikas, this premise may hold for pikas as well. Thus, storing toxic species and delaying consumption until toxins degrade may permit pikas to circumvent an incredible range of potent plant secondary chemicals and broaden their diet without more complicated physiological specializations.

While food-storing animals are confronted with the dilemma that stored foods decay, they also have the rare opportunity to alter the quality of their food. Storing toxic food items and delaying consumption until the food becomes more palatable may be common among food-hoarders. There is anecdotal evidence for this claim, e.g., meadow voles (*Microtus pennsylvanicus*) clip pine twigs and, prior to consumption, leave them lying on the snow for several days during which phenolic concentrations decrease, and gray squirrels (*Sciurus carolinensis*) store acorns with high tannin concentrations while they consume acorns low in tannins (Smallwood and Peters 1986; Roy and Bergeron 1990). Even carnivores may manipulate toxin levels in animal prey: loggerhead shrikes (*Lanius ludovicianus*) prefer stored lubber grasshoppers (*Romalea guttata*) over fresh ones (Yosef and Whitman 1992). Lubber grasshoppers sequester high levels of phenolics and other plant secondary compounds, and it is possible these compounds decline in concentration dur-

ing storage (Yosef and Whitman 1992). If manipulation of toxins by consumers is as frequent as it appears, it adds a new layer of complexity to the definition of food quality, especially for food-storing animals.

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