The Manipulation of Plant Toxins by a Food-Hoarding Herbivore, Ochotona Princeps
Author(s): M. Denise Dearing
Source: *Ecology*, Vol. 78, No. 3 (Apr., 1997), pp. 774-781
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/2266057
Accessed: 21/05/2013 17:48

THE MANIPULATION OF PLANT TOXINS BY A FOOD-HOARDING HERBIVORE, *OCHOTONA PRINCEPS*

M. Denise Dearing[1]

Biology Department, University of Utah, Salt Lake City, Utah 84112 USA

Abstract. Generalist mammalian herbivores typically avoid plant species containing high levels of plant secondary compounds because generalists are thought to lack the ability to process large quantities of these chemicals. Here I propose and test two hypotheses: (1) that food-hoarding herbivores behaviorally overcome consumption limits imposed by secondary compounds by storing food until the toxins degrade; and (2) that the presence of secondary compounds in cached plant material facilitates the preservation of these items, as well as other cached items that lack such compounds. To evaluate these hypotheses, I conducted a number of field and laboratory experiments using the North American pika, *Ochotona princeps,* a generalist herbivore that consumes low-phenolic vegetation in the summer while it simultaneously collects and stores high-phenolic vegetation for subsequent consumption during winter.

In experiments investigating decomposition of summer and winter diets of pikas, after 10 mo of storage, the winter diet retained 20.5% more biomass, and was higher in energy, lower in fiber, and equal in nitrogen compared to the summer diet. Moreover, a common food item in the winter diet, *Acomastylis rossii,* which contains high levels of phenolics, was the only plant extract to deter bacterial growth in a bioassay. *Acomastylis rossii* leaves with experimentally reduced phenolic levels retained significantly less biomass than leaves with natural phenolic concentrations. However, the presence of *A. rossii* in artificial caches containing a low-phenolic species, *Trifolium parryi,* did not facilitate the preservation of *T. parryi.*

Approximately halfway through the typical storage period, phenolic concentrations of pika winter diet samples in artificial caches decreased to levels readily consumed by pikas in their summer diet. Examination of natural haypiles of pikas before and after storage revealed that pikas do increase their intake of *A. rossii* from the haypile sometime during the winter. In experiments with captive pikas, pikas preferred *A. rossii* with experimentally reduced phenolic concentrations over those with natural concentrations. Observations of pikas foraging from natural and artificial haypiles suggested that pikas do not increase their intake of *A. rossii* from the haypile until phenolics levels decrease. Taken together, the results support both of the hypotheses. Pikas manipulate plant chemistry by storing plants rich in allelochemicals and by delaying consumption of these plants until the toxins decay. Moreover, plants with high levels of secondary compounds exhibit superior preservation qualities so that more biomass and nutrients are retained during storage. As food caching is a common strategy among several animal classes and many foods contain potentially deleterious compounds, the manipulation of food toxins by storage may be a prevalent phenomenon.

Key words: bacterial inhibition; decomposition; Ochotona princeps; *phenolics; pikas; plant–herbivore interactions; toxin manipulation.*

INTRODUCTION

The factors governing diet selection of mammalian herbivores have puzzled ecologists for decades. Although numerous field and laboratory studies have been conducted (e.g., Marquis and Batzli 1989, Meyer and Karasov 1989, Willig and Lacher 1991, Dearing 1995), no single set of food quality variables universally predicts diet selection by generalist mammalian herbivores. One axiom emerging from these studies is that generalist herbivores ingest a limited quantity of plants that produce high concentrations of secondary compounds because they are physiologically unable to contend with large quantities of these chemicals (Freeland and Janzen 1974, Bryant and Kuropat 1980, McArthur et al. 1991). However, anecdotal evidence suggests that a subset of mammalian herbivores, the food-hoarding ones, may be able to circumvent physiological constraints in processing plant secondary chemicals by storing food prior to consumption (Roy and Bergeron 1990, Dearing 1995).

Decomposition is an inevitable consequence of food storage (Smith and Reichman 1984). Abiotic and biotic processes can cause the nutritional contents of stored food items to decline (Post 1992). The secondary compounds in harvested plant materials are also subject to these degradation processes (Swift et al. 1979, Waterman and Mole 1994), and therefore may decrease to acceptable levels during storage. Thus, although food caching is typically detrimental to food quality, storage may actually enhance characteristics of a diet consisting of plants laden with secondary compounds.

Additionally, the presence of plant secondary compounds may promote preservation of the cache. The phenolic and sesqueterpene compounds produced by many plants exhibit antifungal and antibacterial activities that retard decomposition (Swain 1979, Swift et al. 1979, Waterman and Mole 1994). For example, leaf litter decay is demonstrably slower in leaves high in these compounds (Swift et al. 1979, Stout 1989). Herbivorous animals that hoard food may take advantage of these natural preservatives by biasing their cache with plants high in these chemicals. Moreover, stored plant material with high concentrations of secondary compounds may facilitate the preservation of other plants in the cache lacking such compounds.

Thus, for generalist herbivores that hoard food, factors influencing the selection of a diet that is cached prior to consumption may differ significantly from those influencing selection of one that is consumed immediately. I propose that herbivores may selectively cache plants high in secondary compounds either to avoid deleterious effects or to take advantage of natural preservative properties of secondary chemicals. It is possible that both of these strategies are fundamental in diet choice as each yields a different benefit to the food hoarder. If secondary compounds degrade during storage, a food otherwise unusable may be rendered palatable, thereby enabling food hoarders to increase usage of species containing secondary compounds. If plants with high concentrations of secondary compounds promote cache preservation by retarding degradation of nutritional compounds, the hoarder receives a greater return for every unit cached. Here I present experimental tests of two hypotheses: (1) that diets high in secondary compounds preserve better (enhanced preservation hypothesis); and (2) that concentrations of secondary compounds decrease to acceptable levels during storage (toxin-reduction hypothesis).

I tested the toxin-reduction and enhanced preservation hypotheses with the North American pika (*Ochotona princeps*: Lagomorpha). *Ochotona princeps* is a generalist herbivore restricted to high-elevation talus slopes in North America (Broadbrooks 1965, Millar 1974). Pikas do not hibernate; to survive the lengthy alpine winters, individuals cache summer vegetation ("haypiles") for winter provisions (Broadbrooks 1973, MacArthur and Wang 1973). The average size of the haypiles is 28 kg of fresh vegetation per pika, repre-

senting ≈14 000 collecting trips during 8–10 wk of the summer (Dearing 1995). The composition of plant species in the haypile differs significantly from the diet consumed during the caching period (Huntly et al. 1986, Dearing 1995). Thus, pikas simultaneously select two different diets, a summer diet that is consumed immediately, and a winter diet that is stored prior to consumption. Neither differences in nutritional content nor plant morphology explain the disparity between summer and winter diets (Dearing 1997a). However, concentrations of phenolic compounds are significantly greater in the winter diet (Dearing 1997a). A single food type, alpine avens (*Acomastylis rossii*) leaves, comprises 50–75% of the winter diet, and contains high concentrations of hydrolyzable tannins. *Acomastylis rossii* leaves are incorporated far less frequently in the summer diet, comprising only 15–22% of the summer diet (Dearing 1995). Pikas ingesting a diet of 25% *A. rossii* leaves exhibit lower levels of fiber and protein digestion and excrete higher concentrations of detoxification metabolites in the urine compared to pikas consuming a diet without *A. rossii* (Dearing 1997b).

To distinguish between the toxin-reduction and enhanced preservation hypotheses, I tested the following predictions of each model. If the superior preservability of plants high in secondary compounds influences diet selection for the winter diet, then (1) the winter diet should preserve better than the summer diet; (2) extracts of plants in the winter diet should exhibit antibacterial properties; and (3) if certain species are collected primarily as preservation facilitators, then their presence should enhance biomass retention of species low in secondary compounds. If pikas select plants high in secondary compounds, e.g., *A. rossii,* and delay consumption until the toxins decay, then (1) toxins should decrease to acceptable levels during storage; (2) pikas should be capable of distinguishing between plants with high and low concentrations of phenolics and should prefer the latter; and (3) plants initially high in secondary compounds should be consumed from the cache after secondary compound concentrations decline.

METHODS

Study site and organism

All field work was carried out on the Long Term Ecological Research site on Niwot Ridge, Nederland, Boulder County, Colorado (40°03′ N, 105°36′ W). The site was above treeline, on the eastern slope of the West Knoll (elevation 3500 m). The plant community was alpine meadow; dominant species were *Silene acaulis, Acomastylis rossii, Deschampsia caespitosa,* and *Carex* species. Fresh vegetation was available at this site during July and August only; there were no evergreen species.

Pikas are territorial and solitary; each individual collects vegetation for its own cache, or haypile (Smith

TABLE 1. Percentages of different food items in the summer and winter diets used in the artificial haypile experiment. Percentages are based on dry masses. Diets were generated from 500 observations of seven pikas consuming summer diet or collecting winter diet. Graminoids represent both *Carex* species and *Deschampsia caespitosa*.

Food item	Winter diet	Summer diet
Acomastylis rossii leaves	69.0	9.8
Graminoids	2.1	21.5
Bistorta bistortoides leaves		9.2
Bistorta bistortoides flowers	2.5	1.9
Trifolium parryi leaves	6.1	30.0
Erigeron simplex flowers		5.8
Trifolium parryi flowers	2.0	6.3
Silene acaulis leaves		5.8
Acomastylis rossii flowers	12.3	9.8
Artemisia scopularum leaves		2.4
Artemisia scopularum flowers		2.0
Castilleja occidentalis leaves		1.5

and Ivins 1984). During cache construction, pikas clip fresh vegetation and store it under rocks; vegetation is not dried prior to storage (M. D. Dearing, *personal observation*). Pikas may live up to 7 yr and haypile areas tend to be reused by the same individual in successive years (Smith and Ivins 1983; M. D. Dearing, *personal observation*). Pika foraging behavior on the West Knoll was observed during the summers (end of June through mid-August) of 1990 through 1993. Pikas were eartagged with colored washers in unique combinations to permit individual identification by observers with binoculars. Observations were conducted from a 1- 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 of these items. I further distinguished between flowers, pedicels, and leaves within a species. Pikas appeared undisturbed by stationary observers.

I compared the preservability of the summer and winter diets in a decomposition experiment. The contents of winter and summer diet were based on 500 observations of seven pikas consuming and collecting vegetation on Niwot Ridge during June–July 1991 (Table 1). Each artificial haypile contained samples of either winter or summer diet with five 30 g (wet mass) subsamples in individual 1-mm² mesh size nylon litterbags. To prevent pikas and other animals from consuming the samples, all five subsamples were enclosed together in a 1-mm² fiberglass screen bag. Artificial haypiles were replicated eight times per diet and placed randomly on a section of talus near the pika observation site on Niwot Ridge in July 1991. One subsample was drawn from each artificial haypile approximately every 3 mo in July 1991, September 1991, December 1991, March 1992, June 1992. I measured dry mass, total energy (bomb calorimetry) and protein (N as estimated with CHN analyzer × 6.25) on all subsamples. Cellulose and lignin (Van Soest 1963, Goering and Van

Soest 1970) were measured for only four of the artificial haypiles per diet.

A literature survey and initial screening of plants on the study site suggested that phenolics were the most common class of secondary compounds. Therefore, I concentrated my assays of secondary compounds on phenolics (for details, see Dearing 1995). I measured total phenolic concentrations and astringency levels of artificial haypile samples. Phenolics were extracted in 85% methyl alcohol (MeOH) using the homogenization methods of Torti et al. (1995). Total phenolics were measured using the Folin-Ciocalteu assay as described in Waterman and Mole (1994). Astringency was measured using the assay of Hagerman and Butler (1978). Tannic acid was used as a standard for both assays; results are expressed as milligrams of tannic acid equivalents (TAE) per gram dry mass of plant material.

The effect of diet composition on nutritional and phenolic contents was assessed using repeated measures analyses of variance. The haypile contents of energy, nitrogen, and fiber were calculated using two methods. First, to estimate nutrient returns for an initial amount of diet stored, nutritional contents were based on 100 g of diet initially cached. To estimate the nutritional content of the diet during storage, nutritional contents were estimated on a per gram of diet basis.

To determine if any of the plant species available on the Niwot Ridge site produced compounds with antibacterial qualities, I conducted a bioassay using *Bacillus subtilus*, a common soil bacterium. Plant extracts were made for the following species: *Acomastylis rossii, Artemisia scopulorum, Bistorta bistortoides, Carex* sp., *Castilleja occidentalis, Deschampsia caespitosa, Erigeron simplex, Minuartia obtusiloba, Silene acaulis,* and *Trifolium parryi*. Separate extracts were made for leaves and flowers of all dicot species. Plant tissue was ground under liquid nitrogen and secondary compounds extracted in 85% MeOH according to extraction techniques of Torti et al. (1995). The solvent was removed by lyophilization and the pellet brought back to the original volume with distilled water. A quantity of each extract (15 μL) was placed in duplicate on a sterile filter paper disk (2 mm diameter) on a lawn of *Bacillus subtilus*. After 24 h, the radius of the inhibition zone was measured.

To determine if phenolic concentrations affected plant decomposition, I compared decomposition of *A. rossii* with natural levels of total phenolics, 123.7 mg/g TAE, (control) to *A. rossii* with experimentally reduced levels of total phenolics, 0 mg/g TAE (experimental). Low-phenolic *A. rossii* were obtained from a population growing naturally in the shade provided by a building on the study site. Samples of experimental (N = 7) or control (N = 7) *A. rossii* (30 g wet mass) in nylon litterbags (1-mm² mesh), were placed on the talus on Niwot Ridge in July 1992. Samples were retrieved in July 1993, and the percentage of dry mass remaining was compared using a *t* test. Sun and shade leaves of

A. rossii did not vary tremendously with respect to variables other than phenolic content. Nutritional values of sun vs. shade leaves, respectively, were as follows: nitrogen content: 3.04 vs. 3.05%; cellulose: 9.24 vs. 11.5%; lignin: 2.96 vs. 6.00% (Van Soest 1963, Goering and Van Soest 1970); energy: 18 731.768 vs. 17 468.2 J. These analyses were performed in duplicate from homogenized samples of >20 leaves, and are expressed per gram dry mass.

To determine if plant species with high levels of phenolics enhanced the preservation of plant species with low levels of phenolics, differences in biomass decomposition of *T. parryi,* a low-phenolic species, in the presence and absence of *A. rossii,* a high-phenolic species, were assessed in a 3-mo experiment. Treatments consisted of individual 30-g (wet mass) samples of *T. parryi* or *A. rossii* and a combined sample consisting of 15 g (wet mass) of each species placed in nylon litterbags. There were five replicates of each treatment; the experiment was conducted from July 1994 through September 1994.

Prerequisites of the toxin-reduction hypothesis are that pikas are capable of discerning differences in phenolic concentrations between plants, and prefer those with lower phenolic concentrations. To determine whether pikas could differentiate between *A. rossii* with differing phenolic concentrations, I conducted feeding trials with captive pikas. Consumption by pikas of *A. rossii* with reduced concentrations of phenolics was compared to consumption of *A. rossii* with natural phenolic concentrations. Four captive pikas were offered either food for 7 h. After the experiment, any leftovers were dried to a constant mass. Consumption of *A. rossii* with differing phenolic levels was compared using a paired *t* test.

I employed three different approaches to ascertain whether pikas consumed *A. rossii* from their haypiles. The first consisted of direct observations of pikas foraging during the summer from their newly built haypiles. Over four summer seasons (1990–1993), I recorded the plant species and tissue type (flowers or leaves) and the number of these items that pikas consumed while in their haypiles. I also conducted cafeteria-style trials using captive pikas that simulated haypile feeding. In July 1992, five captive pikas were simultaneously presented with 50-g fresh samples of each of the following: *A. rossii* flowers, *A. rossii* leaves, *T. parryi* flowers, *T. parryi* leaves, and *Bistorta bistortoides* leaves and graminoids (50:50 mixture of *D. caespitosa* and *Carex* sp.). After 7 h, all leftovers were removed and weighed. Three 50-g controls of each food type were used to calculate the amount of evaporative water loss that occurred during the trial. Lastly, to determine whether pikas consumed *A. rossii* from their natural haypiles, I monitored during two summers the relative abundances of food types in the haypile immediately before and after storage for haypiles constructed. Eight haypiles were sampled in summer 1990,

and seven haypiles in summer 1991. For each haypile, ≈100 g dry mass was sampled from the haypile at the end of the summer (August) and again, ≈11 mo later immediately following the snowmelt (June). Food types were sorted to flowers, pedicels, and leaves of each species. Results are reported as dry masses. Relative abundances of food types in the haypile before and after storage were compared using paired *t* tests. All pikas included in the analysis survived the winter and were seen again the following summer.

RESULTS

Over a year, the winter diet preserved better than the summer diet with respect to biomass and several nutritional variables (Fig. 1, A–D). At the end of the storage period, the winter diet retained 20.5% more of its biomass than did the summer diet (Fig. 1A, $P = 0.0001$, df = 1, 14). To calculate nutritional returns on the initial investment, nutritional contents were estimated based on an initial 100 g dry mass of stored food. The winter diet was higher in total energy (Fig. 1B, $P = 0.001$, df = 1, 14) and equal to or lower in fiber (Fig. 1C, $P = 0.15$, df = 1, 6) than the summer diet for every unit of diet originally collected. For the majority of the storage period, the protein content of the winter diet was equal to that of the summer diet; in the final sampling period, the protein contents of the winter diet significantly exceeded that of the summer diet (Fig. 1D, $P = 0.44$, df = 1, 14). Thus, the nutritional return on the initial collection investment was higher for the winter diet.

Nutritional contents of the diets were also compared on a per gram basis throughout the winter as the diets decomposed (Fig. 1, lower panel). This assessment represents the nutrient composition of the diet during storage that is available to pikas. Energy contents of the summer and winter diets were approximately equal at all times during storage (Fig. 1E, $P = 0.31$, df = 1, 14). However, differences in fiber content of the summer and winter diets increased during storage. After the first 2 mo of storage, the summer diet always contained significantly more fiber (Fig. 1F, $P = 0.005$, df = 1, 6). The protein content of the winter diet was significantly lower than that of the summer diet for the majority of the storage period (Fig. 1G, $P = 0.0001$, df = 1, 14). However, shortly after storage, the protein content of the winter diet equaled or surpassed the protein content typically consumed in a diet of fresh summer vegetation, i.e., summer diet in July (Fig. 1G).

Of the 11 plant species common at the field site and in the diets, only extracts from *A. rossii* exhibited antibacterial qualities in a bioassay with *Bacillus subtilus.* For independent extracts of leaves and flowers of *A. rossii,* a zone of no apparent bacterial growth extended 4 mm in radius from the edge of the paper discs containing the plant extracts. For all others, bacterial growth was continuous.

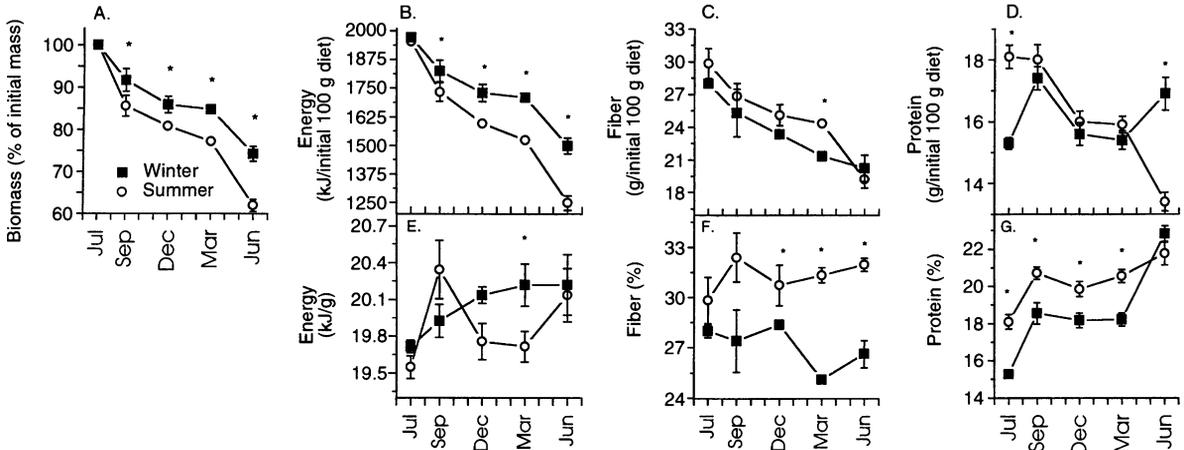Phenolic concentrations affected the decomposition

FIG. 1. Biomass and nutrient contents of summer and winter diets during 11 mo of storage in artificial haypiles. The effect of diet composition on the decomposition, energy, nitrogen, and fiber were assessed using repeated-measures ANOVAs. Overall effects are reported in the text. Asterisks indicate significant differences ($P < 0.05$) between winter and summer diets using least significant differences Bonferroni corrected for multiple comparisons ($n = 5$). Upper panel presents nutritional content based on an initial 100 g dry mass of diet, while the lower panel presents nutrient content per gram or as a percentage of total mass. Thus, the upper panel depicts the nutritional return for each unit of diet collected, while the lower panel is the nutritional content at the sampling period.

of plant biomass during storage. In decomposition experiments, *A. rossii* leaves with reduced phenolic contents lost significantly more biomass during storage than *A. rossii* leaves with natural levels of phenolics ($t = 3.7$, df = 8, $P = 0.02$; Fig. 2). However, the presence of *A. rossii* in artificial haypiles did not facilitate the preservation of other species low in phenolics ($t = 0.66$, $P > 0.05$, $n = 12$, Fig. 3).

Concentrations of plant secondary compounds in the winter diet decreased during storage (Fig. 4). Astringency levels in the haypile decreased 50% within 3 mo after storage, while total phenolic concentrations decreased 50% within 5 mo after storage. Levels of astringency and total phenolics equaled that of the summer diet by February and March, respectively.

In feeding trials, pikas consumed more of the low-phenolic *A. rossii* than the high-phenolic *A. rossii* ($t =$

3.7, $P = 0.02$, $n = 4$). Pikas consumed 3.3 ± 0.14 (SE) g dry mass of the low-phenolic *A. rossii*, vs. 2.2 ± 0.30 (SE) g of high-phenolic *A. rossii*.

There were significant changes in relative abundances of food items before and after storage in the haypile (paired t tests, $P < 0.05$, Fig. 5). Pikas pref-

FIG. 3. Decomposition of haypiles composed of a high-phenolic species, *A. rossii* only (*Aco* only), a low-phenolic species, *Trifolium parryi* only (*Tri* only), and both species combined. The predicted value was generated from the average of *A. rossii* only and *T. parryi* only. Error bars are one standard error.
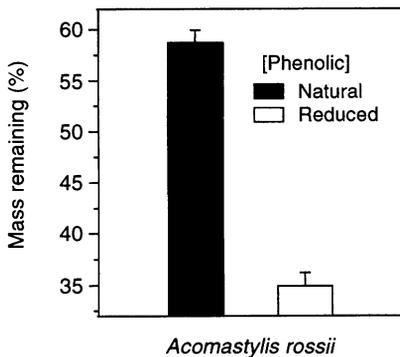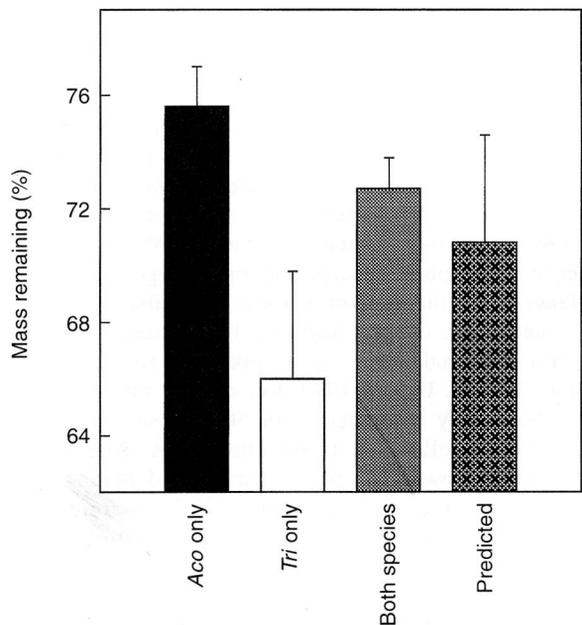

FIG. 2. The percentage of dry mass remaining after 3 mo of storage in artificial haypiles of *A. rossii* leaves with natural phenolic levels, compared to those with experimentally reduced concentrations. Vertical lines are one standard error.
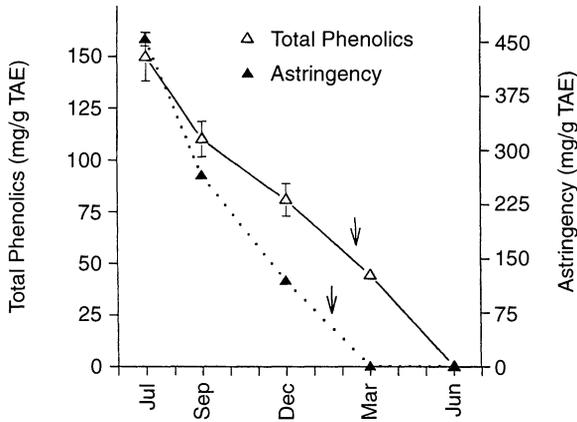
FIG. 4. Two measures of phenolic changes in the winter diet over time. Total phenolics (mg TAE/g dry mass of plant material) are indicated with the solid line, and astringency (mg TAE/g dry mass of plant material) with the dashed line. The total phenolic and astringency concentrations that pikas consume in the fresh summer diet during July and August are indicated with arrows. Error bars represent ±1SE.

erentially foraged during the storage period on the low-phenolic species in their natural haypiles (Fig. 5). Preferred food types included *Bistorta bistortoides* leaves, *Trifolium parryi* leaves, and *Castilleja occidentalis* flowers. Food types avoided by pikas were *A. rossii* flower stems, and graminoids, as these increased in relative abundance in the haypile after storage. Leaves of *A. rossii* were neither preferred nor avoided.

Consumption of *A. rossii* leaves by pikas in natural and artificial haypile situations did not differ from the proportion of *A. rossii* consumed in the summer diet. Over four summer seasons, I observed nine pikas consuming a total of 34 items directly from their haypiles. *A. rossii* leaves comprised 21% of the wet mass of all items combined. For simulated haypiles with captive pikas, 15.1% of the diet consisted of *A. rossii* leaves. In both of these haypiles, the proportion of *A. rossii* consumed was similar to the fresh summer diet; i.e., within the 95% confidence interval around the mean for the summer diet, 18.2 ± 4.6% (Dearing 1995).

DISCUSSION

Pikas appear to gainfully manipulate the secondary chemistry of plants in their haypiles in two fashions. First, the high-phenolic plants selected by pikas for their winter diet caches yielded greater biomass and nutrient returns during the protracted storage period than low-phenolic species consumed during the summer. *A. rossii,* the most abundant species in the winter diet, was responsible for the superior preservation of the winter diet, as high-phenolic plants retained more biomass during storage, and extracts of *A. rossii* phenolics retarded bacterial growth. However, high-phenolic plants did not retard decomposition of other species in the haypile, and so did not function as natural preservatives for other haypile plants. Furthermore, pi-
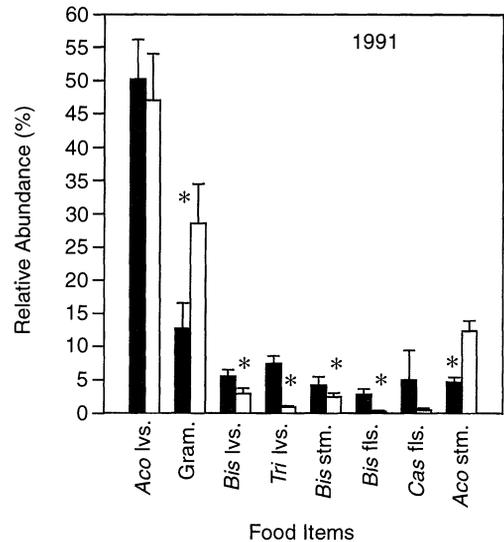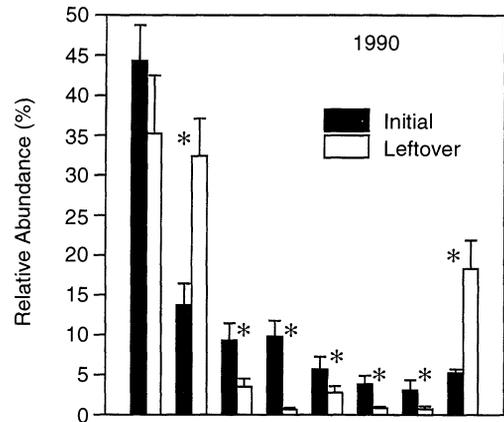

FIG. 5. Relative abundances (percentage of dry mass) of food types before and after winter foraging in haypiles constructed by pikas in 1990 and 1991. Three-letter prefixes are species abbreviations: *Aco, A. rossii*; Gram., *Deschampsia caespitosa* and *Carex* spp. combined; *Bis, Bistorta bistortoides*; *Tri, Trifolium parryi*; *Cas, Castilleja occidentalis.* Suffixes indicate plant part: leaves (lvs.), flower heads (fls.), and flower pedicels (stm.). Asterisks indicate significant differences in relative abundances of food items before and after storage ($P < 0.05$).

kas preferentially cached plant species that were too noxious for immediate ingestion, and delayed consumption of these plants until the toxins degraded to palatable levels. Thus, I found evidence for both of the proposed hypotheses: that high-phenolic plants preserve better, and that pikas delay consumption of high-phenolics species until phenolic levels decrease over time.

The winter diet preserved better with respect to both total biomass and nutritional contents than did the summer diet. To a pika, the difference in potential losses of biomass between the summer and winter diets represents the equivalent of 3000 foraging trips or 70 d

of food (Dearing 1995). The high-phenolic content of *A. rossii* combined with the large proportion of *A. rossii* in the winter diet appeared to be the basis of the winter diet's superior preservability. *Acomastylis rossii* leaves with high concentrations of phenolics retained more biomass during storage than *A. rossii* leaves with low levels of phenolics. Additionally, of 11 plant species examined, only extracts from *A. rossii* manifested antibacterial qualities. However, *A. rossii* did not facilitate the preservation of other cached plant material with low levels of phenolics. Taken together, these results imply that *A. rossii* was collected for the haypile as a potential food item, and not as a natural preservative for other haypile plants.

There was also evidence for the hypothesis that pikas delay consumption of toxic plants until toxin concentrations decrease. From March until the end of June when fresh vegetation appears, phenolic concentrations of the winter diet were as low as that found in the fresh summer diet. The quality of the haypile in the spring may be crucial, because mating and reproduction take place in May underneath the snow (Millar 1972, Smith 1978).

Support for the toxin-reduction hypothesis is contingent on pikas perceiving differences in phenolic concentration and responding appropriately. Several lines of evidence suggest that pikas monitor phenolic concentrations and delay consumption of plant species initially high in phenolics until after phenolic concentrations decline during storage. In feeding trials, captive pikas consumed significantly more low-phenolic *A. rossii* leaves than high-phenolic *A. rossii* leaves. This result implies that pikas are physiologically capable of detecting differences in phenolic levels, and prefer plants with lower phenolic concentrations. Additionally, observations of the contents of the winter diet before and after storage demonstrate that even though pikas foraged substantially on cached *A. rossii* during the storage period, they foraged to a greater extent on other species with low-phenolic concentrations. The precise order of consumption of food items from the haypile is unknown. However, changes in the relative abundance of haypile food items before and after storage, combined with observations of both free-ranging pikas foraging from their haypiles during the late summer, and captive pikas foraging on freshly harvested vegetation, imply that the proportion of *A. rossii* consumed during the winter does not increase above that in the summer diet until sometime later in the storage period. This is because pikas foraging from fresh haypiles in the field or in captivity consumed *A. rossii* in the same proportion as in the fresh summer diet ($\approx 18.9\%$). Given that the relative abundance of *A. rossii* did not change in haypiles after storage, while the relative abundances of several other plant species decreased, pikas at some point during the winter must have increased their intake of *A. rossii*, otherwise the relative proportion of *A. rossii* remaining in the haypile

after storage should have increased considerably compared to the initial proportion (Dearing 1995). Moreover, Conner (1983) observed that pikas initially supplement their winter diet by feeding on crustose lichens and tree bark until approximately January, after which they are rarely seen until the spring vegetation emerges in June. Their absence during this interval coincides with the time when the haypile is most nutritious and least toxic.

The preferential stockpiling of toxic species may also benefit pikas by significantly decreasing their risk of predation. Pikas are most susceptible to predation when away from the safety of the talus interstices while foraging and collecting vegetation in the meadow (Ivins and Smith 1983). On Niwot Ridge, pikas forage for the majority of both their summer and winter diets within 1 m of the talus' edge (Dearing 1997a). Given typical length of the meadow–talus interface of individual pikas on Niwot Ridge ($x = 64.3 \pm 5.0$ m, $n = 9$), combined with the plant species composition and available biomass (Walker et al. 1994), the collection of haypiles composed of summer diet would necessitate travel farther from the talus than would be required for a haypile of winter diet. For example, ≈ 10.51 kg (dry mass) of plant biomass (Walker et al. 1994) is available within 1 m from the talus edge of the meadow–talus territory of a pika. *Acomastylis rossii* comprises 25% and *T. parryi* 10% of this available phytomass. The construction of a haypile of summer diet exclusively would require that the absolute amount of *A. rossii* in the haypile would be reduced, leaving ≈ 1 kg of unused *A. rossii* within 1 m of the talus. Furthermore, in this situation the amount of *T. parryi* collected would increase, thereby forcing pikas to extend their foraging radius to at least 2 m from the talus edge. Moreover, to construct a haypile of average size (7.7 kg dry mass), a pika collecting a haypile of summer diet would be required to make an additional 3000 collecting trips to compensate for the summer diet's accelerated decomposition during storage. Thus, construction of a haypile containing initially unpalatable but easily accessible species could substantially decrease predation risk, in that pikas make considerably fewer and shorter foraging trips in the collection of such a cache.

In conclusion, I found support for both of my original hypotheses: plants high in secondary compounds preserved better than those with lower secondary metabolite concentrations, and the concentrations of these compounds decreased to acceptable levels during storage. Ultimately, the nutritional composition of the haypile equaled that of the diet that is consumed fresh during the summer. Thus, the behavior of storing plants rich in secondary compounds has a two-fold benefit, enhancing food preservation and utilizing a less desirable resource. In addition, storing and postponing consumption of toxic plants allows generalist herbivores to circumvent a range of potent plant secondary chemicals without complicated, chemical-specific, physio-

logical specializations (Dearing 1997a). Given that storing food is a typical strategy among several classes of animals, and that many animals store foods that are potentially toxic (Vander Wall 1990), the manipulation of food toxins may be an underappreciated but prevalent phenomenon.

LITERATURE CITED

Broadbrooks, H. E. 1965. Ecology and distribution of the pikas of Washington and Alaska. American Midland Naturalist **73**:299–335.

Bryant, J. P., and P. J. Kuropat. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. Annual Review of Ecology and Systematics **11**: 261–285.

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

Dearing, M. D. 1995. Factors governing diet selection in a herbivorous mammal, the North American pika, *Ochotona princeps*. Dissertation. University of Utah, Salt Lake City, Utah, USA.

———. 1997a. Disparate determinants of summer and winter diet selection in a generalist herbivore, *Ochotona princeps*. Oecologia, *in press*.

———. 1997b. Effects of *Acomastylis rossii* tannins on a mammalian herbivore, the North American pika, *Ochotona princeps*. Oecologia, *in press*.

Freeland, W. J., and D. H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant compounds. American Naturalist **108**:269–289.

Goering, H. K., and P. J. Van Soest. 1970. Forage fiber analyses (apparatus, reagents, procedures and some applications). U.S. Department of Agriculture, Agricultural Handbook Number 379.

Hagerman, A. E., and L. G. Butler. 1978. Protein precipitation method for the quantitative determination of tannins. Journal of Agricultural and Food Chemistry **26**:809–812.

Huntly, N. J., A. T. Smith, and B. L. Ivins. 1986. Foraging behavior of the pika (*Ochotona princeps*), with comparisons of grazing versus haying. Journal of Mammalogy **76**: 139–148.

Ivins, B. L., and A. T. Smith. 1983. Responses of pikas (*Ochotona princeps,* Lagomorpha) to naturally occurring predators. Behavioral Ecology and Sociobiology **13**:277–285.

MacArthur, R. A., and C. H. Wang. 1973. Physiology of thermoregulation in the pika, *Ochotona princeps*. Canadian Journal of Zoology **51**:11–16.

Marquis, J. R., and G. O. Batzli. 1989. Influence of chemical factors on palatability of forage to voles. Journal of Mammalogy **70**:503–511.

McArthur, C., A. Hagerman, and C. T. Robbins. 1991. Physiological strategies of mammalian herbivores against plant defenses. Pages 103–114 *in* R. T. Palo and C. T. Robbins, editors. Plant defenses against mammalian herbivory. CRC, Boca Raton, Florida, USA.

Meyer, M., and K. H. Karasov. 1989. Antiherbivore chemistry of *Larrea tridentata*: effects on woodrat (*Neotoma lepida*) feeding and nutrition. Ecology **70**:953–961.

Millar, J. S. 1972. Timing of breeding of pikas in southwestern Alberta. Canadian Journal of Zoology **50**:665–669.

———. 1974. Success of reproduction in pikas, *Ochotona princeps* (Richardson). Journal of Mammalogy **55**:527–542.

Post, D. M. 1992. Change in nutrient content of foods stored by eastern woodrats (*Neotoma floridana*). Journal of Mammalogy **73**:835–839.

Roy, J., and J. Bergeron. 1990. Branch-cutting behavior by the vole, *Microtus pennsylvanicus*. Journal of Chemical Ecology **16**:735–741.

Smith, A. T. 1978. Comparative demography of pikas (*Ochotona*): effect of spatial and temporal age-specific mortality. Ecology **59**:133–139.

Smith, A. T., and B. L. Ivins. 1983. Colonization in a pika population: dispersal versus philopatry. Behavioral Ecology and Sociobiology **13**:37–47.

Smith, A. T., and B. L. Ivins. 1984. Spatial relationships and social organization in adult pikas: a facultatively monogamous mammal. Zeitschrift fur Tierpsychologie **66**:289–308.

Smith, C. C., and O. J. Reichman. 1984. The evolution of food caching by birds and mammals. Annual Review of Ecology and Systematics **15**:320–351.

Stout, R. J. 1989. Effects of condensed tannins on leaf processing in mid-latitude and tropical streams: a theoretical approach. Canadian Journal of Fisheries and Aquatic Science **46**:1097–1106.

Swain, T. 1979. Tannins and lignins. Pages 657–718 *in* G. A. Rosenthal and M. R. Berenbaum, editors. Herbivores their interactions with secondary plant metabolites. Academic Press, San Diego, California, USA.

Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley, California, USA.

Torti, S. D., M. D. Dearing, and T. A. Kursar. 1995. Extraction of phenolics: a comparison of methods. Journal of Chemical Ecology **21**:117–125.

Vander Wall, S. B. 1990. Food hoarding in animals. University of Chicago Press, Chicago, Illinois, USA.

Van Soest, P. J. 1963. Use of detergents in the analysis of fiberous feeds. II. A rapid method for the determination of fiber and lignin. Journal of the Association of Official Agricultural Chemists **46**:829–835.

Walker, M. D., P. J. Webber, E. H. Arnold, and D. Ebert-May. 1994. Effects of interannual climate variation on aboveground phytomass in alpine vegetation. Ecology **75**:393–408.

Waterman, P. G., and S. Mole. 1994. Analysis of phenolic plant metabolites. Blackwell Scientific, Oxford, UK.

Willig, M. R., and T. E. Lacher, Jr. 1991. Food selection of a tropical mammalian folivore in relation to leaf nutrient content. Journal of Mammalogy **72**:314–321.